Sense in Sensitivity: Assessing Species Vulnerability to Climate Change

Amy McDougall

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Abstract

This thesis investigates the impact of future climate change upon species vulnerability. Reports of shifts in species distributions are already numerous, but the pattern of change is not fully understood. This thesis looks to predict which species are likely to be most at risk under climate change and why? This thesis takes the equation; Vulnerability= Sensitivity + Exposure to better discover which species are most vulnerable to climate change. Additionally, this research explores how mitigation has a role in determining the degree to which species are vulnerable in the future.

Determining a specie's vulnerability to climate change required the creation of values representing each side of the equation, both a measure of sensitivity and exposure. The construction of a sensitivity measure required the creation of a life history and ecological traits database, and required the use of multiple methods of statistical analysis. Exposure was calculated using projections of future suitable climate space created using species distribution model Maxent. To explore the impact of mitigation on species vulnerability exposure was calculated under a range of climate change scenarios. The sensitivity and exposure scores are synthesised into a measure of vulnerability.

The result of the equation, Vulnerability= Exposure + Sensitivity, has revealed which Mammal species are most vulnerable; those which will be exposed to a high degree of climate change and which life history and ecological traits make them sensitive. The most vulnerable species are those which are highly exposed and which have 'slow' life history traits, are range restricted, or, are climate specialist. The regions in which species are identified as most vulnerable include the Neotropical and Afrotropical zones. Mitigation is found to reduce potential vulnerability with early mitigation being the most beneficial. The deeper understanding gained through this research will help us prioritise species for conservation based on their vulnerability.

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1 Introduction

The phenomenon of Human-induced climate change has been recognised for several decades. The first global assessment of climate change and its observed and predicted future impacts was completed by the IPPC in 1990 (IPPC 1990). Over the past 100 years global mean temperature has risen by 0.6°C (Fischlin *et al* 2007) and is projected to rise between 2-6°C during this century (Fischlin *et al* 2007). The influence of climate change on biodiversity is widely recognised, with observations of i) shifts in species phenology(Walther *et al.* 2002; Parmesan and Yohe 2003), ii) shifts in species ranges and associated changes in abundance and extinction risk (Walther 2002; Root 2003); iii) disruption of ecological interactions (Tylianakis 2008) and iv) changes in primary productivity (Fischlin *et al* 2007). It is acknowledged that climate change is altering the context in which we consider conservation planning (Pressey *et al* 2007) thus, the challenge for biologists is to identify potential approaches to mitigate future biodiversity loss (Helmuth *et al.* 2005).

The recognition that biodiversity is at risk from future climate change has led to a proliferation of studies investigating the observed impacts of recent climate change, and the projected future impacts of climate change on biodiversity (Walther 2002). One method commonly used in the prediction of future impacts are species distribution models. These are statistical or mechanistic models which seek to describe how species distributions are realised using physiological and environmental parameters (Guisan and Zimmermann 2000). The hypothesised relationship between species distributions and the environment form the basis for the statistical species distribution models (Pearson 2003) that are of most interest in this study. These models are particularly attractive because of their ability to provide testable hypotheses of species distributions (Guisan and Zimmermann 2000), which is particularly relevant in the face of global climate change (Thomas *et al.* 2004). These statistical species distribution models are also popular because they are less data intensive than mechanistic models. They require only observed species occurrence data and environmental variables representing current and projected future climates to run (Pearson 2003).

The relative ease of running species distribution models to project the impacts of future climate change has meant that there are multitude projections of future extinction risk.

These analyses range from individual species to entire taxon and from regional to global biodiversity (Thomas *et al.* 2004; Fischlin *et al.* 2007)). Projections of future global extinctions estimate that 20-30% of species experiencing 2-3°C warming above pre-industrial levels will be increasingly at risk of extinction (Fischlin *et al.* 2007). Large variation among regional biota means that this extinction figure may be as low as 1% and as high as 80%. (Fischlin *et al.* 2007). It has been predicted that between 25% and 40% of existing ecosystems will undergo significant and recognisable change by 2100 (Fischlin *et al.* 2007). Extinctions and local extinctions are predicted to be especially prevalent among range-restricted or isolated species and populations (Fischlin *et al.* 2007). Each of these studies builds on our understanding of the impacts of future climate change. However, there is recognition that species distribution models only go part way in describing the likely impacts of climate change and overlook significant and ecologically-relevant processes (Pearson & Dawson 2003; Thuiller 2004; Austin 2007).

These ecologically-relevant processes include large-scale alternative drivers of biodiversity change, such as land use changes, resource exploitation and pollution (Brooks et al 2002). Importantly, they also include intrinsic species mechanisms including local adaptation, dispersal capacity and phenotypic and genetic adaptations (Williams et al 2008). Understanding the complexity of species' distributions is notoriously difficult, accounting for all of these processes is beyond the scope of current techniques (Fielding and Bell 1997; Dormann 2007). However, attempts have been made to characterise some of these processes within the current bounds of modelling techniques.

Recently, the focus in correlative modelling has been on the incorporation of alternative drivers. Focusing on incorporating environmental change and biotic processes which interact with climate change, and their effect on species' future range shifts (Pearson and Dawson 2003). These alternative drivers and processes involve the inclusion of land cover data, demography, dispersal capacity, and biotic interactions (Heikkinen *et al.* 2006; Wiens *et al.* 2009). Thus, these hybrid-models incorporate mechanistic properties into normally static correlative models to add further realism to these projections and to reduce uncertainty (Heikkinen *et al.* 2006).

Models provide relevant hypotheses when examining the complexities of biological patterns (Guisan and Zimmermann 2000), conferring valuable insight into how to approach future conservation challenges under climate change (Wiens *et al.* 2009). The current literature encompasses examples of hybrid models projecting the impacts of future climate change on individual species and biodiversity as a whole. However, these examples have mainly focused on representing changes in species distribution based on projections of future climate variables. Therefore do not account for innate species' adaptation capacity and resilience. There are a few studies that have investigated species adaptation or resilience to climate change but these have mainly been limited in scale, concentrating on a few well studied species, or have relied on expert opinion. This thesis aims to account for the impacts of climate change on species distributions whilst also recognising that species have innate characteristics which determine their ability to survive and respond to future climate change.

This analysis has vulnerability theory at its foundation, 'Vulnerability' is a function of three factors; exposure, sensitivity and adaptive capacity (Adger 2006; Williams *et al.* 2008; Dawson *et al.* 2011). In examining the potential of incorporating species' life history and ecological characteristics, Sensitivity, into the assessment of the impact of future climate change this thesis will provide further understanding of this issue. In exploring Sensitivity this study will provide insight into the characteristics which make a species more or less vulnerable allowing the prioritization of those species for conservation which are most vulnerable to future climate change.

Such studies are critical to our understanding of the impacts of future climate change on species biodiversity. They inform and support conservation policymakers and practitioners in their attempts to moderate the impacts of climate change through mitigation and adaptation policy, and conservation planning.

1.1 Research Objectives

This thesis will contribute evidence to the assessment of climate change impacts on biodiversity, highlighting the terrestrial mammal species projected to be most and least vulnerable and the attributes which determine this vulnerability. Previous research, as reviewed in Chapter Two, has concentrated on the observed and predicted impacts of climate change by considering individual species' climate change exposure. Although, it is recognised that species have particular attributes which impact their capacity to persist under climate change, these have rarely been investigated. This thesis contributes timely evidence on this question of whether species can persist under climate change, providing a holistic approach to the assessment of risk to species from climate change. It provides targeted assessment of individual species of Mammals vulnerability to future climate change whilst also providing theoretical evidence concerning the life history and ecological traits which confer sensitivity.

There are three hypotheses relevant to investigation of the impact of future climate change on species biodiversity:

1) That species possess a unique tolerance to climate change shaped by their life histories and ecological traits i.e. its sensitivity. A species' sensitivity influences the species' potential response to future climate change by partially determining the level to which they are vulnerable.
2) That the species' sensitivity to future climate change is likely to affect the species future available climate space, its potential distribution, and will determine how vulnerable that species is to climate change.
3) That the degree to which a species is vulnerable to climate change will be partially governed by the amount of climate change to which it is exposed in concert with its unique tolerance to climate change. Consequently, mitigation of climate change impacts by reducing greenhouse gas emissions will lessen the degree to which a species is vulnerable.

These hypotheses are neatly described in the equation:

$$Vulnerability = f(Exposure \,\&\, Sensitivity)$$

Where Sensitivity describes the species' innate tolerance to future climate change and where the term Exposure describes the degree to which it will be exposed to future climate change. When combined with the literature gaps highlighted above, these hypotheses allow the research questions to be framed in detail with relevance to this thesis.

- **Sensitivity: Species Unique Tolerances to Future Climate Change – "**How can species' sensitivity be determined and which life history and ecological traits cause species to be more or less Sensitive?"
- **Vulnerability – "**What effect does knowledge on species' sensitivity have in the assessment of species Vulnerability to future climate change? "
- **Vulnerability and Mitigation- "**Does mitigation of climate change, through the reduction of greenhouse gas emissions, influence species' overall Vulnerability into the future?"

1.2 An Overview of the Thesis

This thesis is divided into six chapters. The following chapter introduces the context in which the foundation of this thesis is based, highlighting the research gaps existing in the literature and the research questions that arise. Chapter Three concerns the development of the Sensitivity measure, including an introduction to the conceptual framework of this Vulnerability analysis, the methods undertaken to create the measure, the results and a discussion of the findings and their importance in defining Vulnerability. A description of the process used to develop the Exposure measure, the creation of the Vulnerability measure and the subsequent analysis of future vulnerability are described in Chapter Four. Chapter Five investigates the impact of mitigation on species' future vulnerability. Chapter Six concludes the thesis with a summary of the key findings and implications for research and policy.

The three Appendices provide contextual information relevant to the Vulnerability equation. They are provided as appendices so that the logical flow of the Vulnerability equation runs as a thread through the main text. However, they should be considered as a valuable addition important for understanding the broader environment in which this thesis sits. Appendix One provides a review of species distribution modelling including model comparison, selection, evaluation and understanding uncertainty. Appendix Two, describes the Maxent Model and provides a case study which explores the effect of changing the Maxent settings. Appendix Three, explores uncertainty associated with climate projections and discuss the potential impact of uncertainty on predictions of future species distributions.

1.3 Conceptual Contribution of this Thesis

This thesis contributes to the literature by taking a holistic approach to exploring the impact of climate change using the basic constructs of Vulnerability theory (Adger, 2006). It explores the precepts of vulnerability outlined by Williams et al (2008), with specific attention to the definition of sensitivity and exposure.

This thesis investigates methods of quantifying levels of species' vulnerability to climate change by creating a method to assess species' sensitivity. This compliments the already well-established measure of Exposure calculated using species distribution modelling. This thesis contributes to the conceptual literature by identifying species' traits which increase vulnerability to climate change and those which promote species' survival and potential to thrive under a changing climate. This thesis contributes to the evidence-base by identifying which species of Mammal are most vulnerable to future climate change.

Further, this thesis explores the impact of mitigation on species' vulnerability an important factor in determining a species vulnerability to climate change (Williams *et al* 2008).

2 Impacts of Climate Change on Ecosystems and Biodiversity

This chapter presents an overview of the academic literature concerning the impact of climate change on biodiversity and ecosystems. It summarises the state of knowledge within this field and highlights research gaps in the literature. This area has a large academic literature although many questions remain to be investigated. This chapter presents the research questions this thesis will answer, highlighting the novelty of this thesis and the contributions to knowledge it will make.

2.1 Ecosystems and Climate Change

Ecosystems are likely to undergo divergent responses to climate change dependent on the extent to which they are already degraded, and the degree of future climate change they are likely to experience (Fischlin *et al.* 2007). There is already evidence that the structure and dynamics of ecosystems are being redrawn as species adapt, disperse or become locally extinct (Walther *et al.* 2002). Dynamic and structural changes in terrestrial ecosystems have been observed including decoupling of coevolved interactions, changes in community composition, impacts of direct warming, and loss of habitat due to altered weather patterns, increased fire frequency, sea-level rise and glacial recession (Walther 2010).

It is forecast that between 25-40% of existing ecosystems globally will undergo significant and recognisable changes by 2100AD (representative of 3.2-4.4°C warming respectively) (Fischlin *et al.* 2007). This loosely corresponds with the projection that under a scenario representing 2.0-5.4°C warming between 10-48% of terrestrial surfaces will encounter novel and disappearing climates by the same period (Williams, Jackson and Kutzbacht 2007). Unique and currently threatened ecosystems will become increasingly vulnerable under climate change, with a 1.5-2.5°C rise in global mean temperature from 1990 levels predicted to move many of these ecosystems into a high risk state (Smith *et al.* 2009).

During the recent past and to the present time ecosystem-degradation has been driven by a variety of non-climatic stressors, natural and human-induced, direct and indirect. Habitat fragmentation, overexploitation and pollution can be considered as direct drivers, whilst human population change and socio-political changes are indirect (MEA 2005). Climate change, therefore, must not be thought of as acting in isolation, but occurring in concert with these stressors (Fischlin *et al.* 2007).

For example, over the past 50 years humans have affected ecosystems more rapidly and on a wider scale than any comparable period in our history (MEA 2005). Land use changes have had, and continue to have the most detrimental impact on terrestrial biodiversity (Sala *et al.* 2000). The degree of past degradation of ecosystems means that the modern landscape holds little inherent capacity for ecosystems to adapt under rapid environmental changes (Walther *et al.* 2005). Centres of endemism, the world's biodiversity hotspots, are already recognised as being disproportionately threatened by human activities (Brooks *et al.* 2002). The additive pressure of climate change on these already vulnerable ecosystems could serve as a tipping point beyond which these ecosystems can no longer recover or adapt (Lenton *et al.* 2008).

Ecosystems are dynamic entities which have the potential to transition through different states (Walther 2010). The term 'tipping point' describes the critical threshold beyond which a system is no longer stable and will undergo transition to an altered and potentially novel state (Fischlin *et al.* 2007; Lenton *et al.* 2008). These transitions can be rapid (1-10yrs), gradual (50-100yrs) or slow (300yrs+) (Lenton *et al.* 2008). The restriction of this natural flux within the system, i.e. through habitat loss and fragmentation, might ultimately reduce the ecosystems adaptive capacity (Folke *et al.* 2004). Transitions in some systems are expected to be triggered with warming of 1°C to 2°C, with several more being triggered as global warming ranges upward towards 3°C to 5°C (Ramanathan and Feng 2008). Climate change is expected to at the least perturb ecosystems toward their tipping points, if not to ultimately cause the transition (Fischlin *et al.* 2007).

Several large-scale ecosystem and meteorological components which are liable to exceed their natural stable state and transition under climate change have been identified (Lenton *et al.* 2008). These components have been termed, 'tipping elements' and include, but are not limited to, the Amazon rainforest, the Sahel/Sahara and the West African Monsoon, Arctic summer sea ice and the El Niño southern oscillation (ENSO). One such example, is the Amazon rainforest, where warming of 3-4°C is predicted to limit the forests' ability to re-establish, as a product of a reduction in precipitation, an increase in summer temperatures and the length of the dry season, the result of which is forest dieback (Lenton *et al.* 2008). The consequence of forest dieback is in this case predicted to be a decrease in biodiversity and further reduction in precipitation(Lenton *et al.* 2008). At a more localised scale changes in species assemblages can also trigger ecosystem transitions, or even complete ecosystem collapse, by undergoing rapid transition to species-poor, less productive assemblages (Fischlin *et al.* 2007). The consequence of which has implications beyond the bounds of the ecosystem because assemblages of species in ecosystems not only reflect interactions among organisms but also between organisms and the abiotic environment (Walther *et al.* 2002). In many cases, however, the proximity of an ecosystems current state to ecosystem-specific critical-thresholds is unknown (Fischlin *et al.* 2007).

The Paleoecological Record

There is general agreement that climatic regimes have influenced species' distributions (Walther *et al.* 2002). Over past millennia distributions fluctuated between range expansion and contractions as a species experienced glacial cycling (Walther *et al.* 2002). Often a species' distribution is the result of oscillations in temperature and precipitation, where these fluctuations confer an advantage or disadvantage to a species. Past episodes of climate change have differed in the rate and extent to which they occurred, however, across the paleoecological record there is corresponding evidence that species assemblages have changed with novel communities arising in their stead (Williams and Jackson 2007; Williams, Jackson and Kutzbacht 2007; Prentice *et al.* 2011). Although past climate change events have occurred at a slower rate than that predicted for the 21st century, observations exist of abrupt and non-linear changes in terrestrial systems associated with these periods (Williams *et al.* 2011).

2.1.1 **Global Change Drivers**

Climate change will exacerbate the threat to biodiversity, in and of itself, but also in concert with a series of other global change, often human-mediated stressors (Fischlin *et al.* 2007). The main drivers of global change are; climate change, land-use change,

CO_2 enrichment, nitrogen deposition and species invasions (Tylianakis *et al.* 2008)., Their associated impacts are well documented in isolation, but their collective effects are less well researched (Leuzinger *et al.* 2011). These drivers, although occurring in consort, have the potential to have non-additive impacts. (Leuzinger *et al.* 2011). Leuzinger *et al* (2011) analysed the impact of multiple stressors (Ozone, CO_2, water availability and temperature changes) on factors such as total biomass, carbon and nitrogen deposition at 160 climate manipulation sites. They reported a reduction in the negative impact of the factors when analysed in combination compared to the factors affected in isolation. The accumulation of stresses can quickly degrade the systems resilience making them vulnerable to replacement by better adapted ones (van Vliet and Leemans et al 2006). Degradation can occur rapidly, within days to decades, but recovery is often very slow, taking decades to millennia, and is frequently hampered by other stressors (van Vliet and Leemans 2006). The complexity in understanding how these drivers interact challenges our ability to predict their effect on future responses to climate change (Tylianakis *et al.* 2008). This section reviews the drivers and stressors which often act alongside climate change in mediating global change.

Changes in CO_2, Nitrogen Deposition and Tropospheric Ozone

Rises in atmospheric CO_2, nitrogen deposition and tropospheric ozone are highly intertwined with climate change (Tylianakis *et al.* 2008). By 2100AD it is predicted that ecosystems will experience atmospheric CO_2 levels higher than at any point in the past 650,000 years (Fischlin *et al.* 2007). Human activity has roughly doubled the yearly creation of reactive nitrogen since preindustrial times (MEA 2005). All three interact with plants physiological processes and evidently will have acute implications for the global carbon cycle with consequences for terrestrial and water-based ecosystems (MEA 2005). The increasing addition of CO_2 and nitrogen into the atmosphere has the effect of increasing short-term plant growth, a process known as CO_2 fertilisation (Tylianakis *et al.* 2008). These physiological changes may increase the resilience of individual species to other stressors, such as higher temperatures, drought and ozone (Tylianakis *et al.* 2008). However, the interaction of nitrogen with other factors is strong and multifaceted, particularly in relation to the complex dynamics of the carbon, nitrogen and phosphorus cycles (Tylianakis *et al.* 2008). For example, it is important to note that the CO_2 fertilisation effect has been found to be nitrogen-limited, lessened in mature trees and over time reduced due to acclimation (Tylianakis *et al.* 2008). Conversely, the rise in tropospheric ozone (O_3) over the past 160 years, mainly through anthropogenic emissions and to a lesser degree climate change, is known to negatively affect tree growth, by reducing the plants ability to photosynthesise and assimilate carbon (MEA 2005). Forests are currently a net sink for both CO_2 and O_3, however warming may increase both gases beyond the capacity of trees to absorb them, causing forests to become a net source (MEA 2005). Terrestrial ecosystems, particularly forests (Fischlin *et al.* 2007), store carbon, approximately three times more efficiently than the atmosphere does, this carbon sink is likely to become saturated mid-century (Lucht *et al.* 2006) and become a net source of carbon releasing it into the atmosphere by the century's end (Levy *et al.* 2004; Scholze *et al.* 2006).

Change in Land-use and Cover

Over the past 50 years humans have affected ecosystems more rapidly and on a wider scale during any comparable period in our history (MEA 2005). There are few ecosystems in which human activity hasn't had an impact (MEA 2005). Land use change continues to have the most detrimental impact on terrestrial ecosystems and their associated biodiversity, due to habitat loss and fragmentation (Sala *et al.* 2000). This trend is predicted to continue into the future (MEA 2005).

Deforestation to make way for agriculture is not only impeding forest ecosystems' ability to provide but also has accounted for a quarter of all anthropogenic CO_2 release (Fischlin *et al.* 2007). Land-use and cover change influences climate change, through changes in sinks and sources of CO_2 and changes in the relative absorption of radiation by the land surface (Fischlin *et al.* 2007). Land-use change has also been found to reduce rainfall, and trigger changes in precipitation patterns as a result of conversion of forests to pastures (MEA 2005).

Invasive and Alien Species

Over the past decade an increase in the rate of spread of invasive species has been observed, and evidence suggests that climate change effects have augmented this expansion in range (Thomas, 2004; Hellman et al, 2008). Species, including plants, animals and pathogens, have been observed exceeding their historical ranges as climatic conditions becomes more attuned to their habitat requirements (Tylianakis *et al.* 2008). Invasive alien species are of particular concern as they often detrimentally impact native biodiversity (Vitousek *et al.* 1996; Rödder and Weinsheimer 2009). Invasive species are often able to outcompete native species, for example through their greater ability to exploit prey or nutrients, however, it is thought that invasive species are likely to cause extinctions through trophic as opposed to competitive interactions (Tylianakis *et al.* 2008). There are several recognised traits that invasive species possess, for example they are mainly generalists; having broad dietary and habitat niches (Rödder and Weinsheimer 2009) and they often have a high reproductive rate, are fast growing and are successful dispersers (Vitousek *et al.* 1996). The successful establishment of non-native species into an ecosystem requires a suite of favourable conditions (i.e. climate and food availability) and is often dependent on the presence of competitors and predators, and the degree of human disturbance (Rödder and Weinsheimer 2009). Disturbances, such as extreme events, may create such favourable conditions, by opening up the landscape for colonisation (Connell and Slatyer 1977). The expansion of invasive species will trigger the re-organisations of communities and result in the formation of novel ecosystems and interactions (Rödder and Weinsheimer 2009). One observed effect of recent climate change is that species are colonizing previously ‘cool’ regions, as environmental conditions begin to fall within these species niche requirements; an phenomenon particularly prevalent in the arctic, where arctic specialists ranges are contracting (Parmesan and Yohe 2003).

2.1.2 **Impact of Climate Change on Terrestrial Ecosystems**

The species composition of an ecosystem is determined by the individual species’ physiological tolerances to the climate at its specific location, the interactions among organisms (i.e. interspecific competition, predator-prey) and those between organisms and the abiotic environment (Walther *et al.* 2002; Williams *et al.* 2008). Changes in species behaviour and distribution will not occur in isolation having far reaching consequences across the ecosystem in which they appear (Walther 2010). Three key factors have been identified which are thought will affect the way in which species react to climate change (Helmuth *et al.* 2005). Firstly, the relative importance of the environmental variables which limit a species' geographic or local distribution will flux in space and time (Helmuth *et al.* 2005). Second, a species' physiological ability to endure and recover from environmental stress can vary radically in time and space (Deutsch *et al.* 2008). And thirdly, climate change is inherently variable; it will not purely produce an increase in average global temperature, but vary weather patterns, such as precipitation, spatially, daily and seasonally (Helmuth *et al.* 2005). These factors will determine whether a species will be vulnerable to new conditions, or able to adapt independently and flourish (Williams *et al.* 2008).

Disturbance Regimes

The predicted increase in extreme events associated with climate change is expected to further compromise species' abilities to survive and reproduce (Kearney and Porter 2009). In the recent past observations suggest that extreme weather events have changed more markedly than average weather, and thus have elicited stronger responses from ecosystems (van Vliet and Leemans et al 2006). Hot extremes, heat waves, heavy precipitation events and tropical cyclones are all predicted to increase with further warming (Solomon *et al.* 2007). These changes are unlikely to be spatially homogenous and will be characterized by patterns in large scale climate (Meehl and Tebaldi 2004). Climate extremes- linked to natural fluctuations and underlying long-term trends- are the dominant determinant of a species' range, and are an important driver in ecosystem change (Walther *et al.* 2002). Thus, this increase in extreme events has led to climate change impact levels which have exceeded that expected in the early decades of change (van Vliet and Leemans et al 2006). In fact, when linking observed ecosystem responses to recorded changes in weather patterns, van Vliet and Leemans (2006) found most appeared to be relatable to extreme events. Extreme weather events can abruptly change conditions in a species' habitat breaching the species' natural range of tolerances, leading to local mortalities and population extinctions (Hoegh-Guldberg *et al.* 2008). The root cause of degradation and loss of living coral cover, known as coral bleaching, has been identified as the occurrence of extreme ocean temperatures which surpassed the corals physiological tolerances (Hoegh-Guldberg *et al.* 2008).

Disturbance regimen such as fire, avalanche and wind are known to be climatically sensitive, and increases in frequency or severity will be to the detriment of those ecosystems in which they have a controlling impact (Fischlin *et al.* 2007). Ecosystems which are strongly controlled by disturbance regimes, such as savannah and grassland, are likely to experience variation in the timing and degree of disturbances, which has the potential to elicit major changes in the ecosystem structure. For instance, fire exclusion due to a predicted increase in precipitation, has the potential to transform savannah to forest (Fischlin *et al.* 2007). Temperate and boreal forests are projected to exhibit large range shifts under a 3°C rise in global mean temperature, with only 50-86% of these ecosystems remaining stable (Leemans and Eickhout 2004). However, predicted changes in the fire and drought frequency and severity in the short term are likely to be more critical for these ecosystems (Fischlin *et al.* 2007).

2.2 Impacts of Climate Change on Species

A temperature rise between 1-2°C by 2100 is predicted to severely limit adaptive capacity of ecosystems and species within them, escalating the already high rate of biodiversity decline and compromising ecosystem service provision (Leemans and Eickhout 2004).

Species and ecosystem-wide responses to climate change are likely to be non-linear and be observable only after a significant time lag, meaning that we cannot see the full affect that climate change has already had (Parmesan and Yohe 2003). For example, the adverse impact of climate change on individuals may appear minor but exert sizeable impacts on the entire system, through impacting crucial biological interactions between species (Tylianakis *et al.* 2008). The rate of climate change occurring is not equally distributed across the Earth's surface, with some regions experiencing high warming trends (such as the Arctic bioregions) and others experiencing much smaller rates of warming (Burrows *et al.* 2011). Thus, the impact of climate change on ecosystems and biodiversity will also not be equally distributed (Burrows *et al.* 2011). It is predicted that anticipated climate change is likely to disproportionately impact terrestrial species at higher latitudes, in parallel with the rate of warming at these latitudes (Deutsch *et al.* 2008). However, evidence suggests that tropical species are equally vulnerable because they are adapted to persist under a narrow range of environmental conditions (Vamosi and Vamosi 2008). This section reviews the observed impacts and those predicted to occur in association with climate change.

2.2.1 **Phenology**

Global warming, a chief aspect of climate change, is associated with the advancement of species' life history events (Memmott *et al.* 2007). Climate change will alter species' phenologies by 1) speeding or slowing the development rate of species, or by 2) modifying the timing of environmental cues which preclude the appearance of species into the community (Yang and Rudolf 2010). Many examples have been recorded which show that significant changes in species phenologies have occurred in relation to climate change (van Vliet and Leemans et al 2006). These phenological changes have concerned shifts in timing of migration, flowering, egg laying and developmental rate, (Root *et al.* 2003) and have included species across all the major taxonomic groups (Parmesan 2007). Parmesan (2007) estimated a mean advance in phenological events, across plants and animals, of 2.8 days (±0.35/ 203 species) per decade.

Phenological responses to climate change have been particularly strong in higher latitudes which have warmed more than lower latitudes (Root *et al.* 2003), and more such shifts are reported for Northern hemisphere species than for the Southern hemisphere species (Root *et al.* 2003). The phenological advances resulting from a constant rate of warming will be highly variable due to the physiological constraints of the species in question (Angilletta 2009), as well as the location. Species' phenological responses show considerable variation across the community (Yang and Rudolf 2010). This is apparent at the large scale across the taxonomic classes where the average advancement in phenology for Amphibians is 7.6 (±3.09) days but for Birds is 3.7 (±0.70) (Parmesan 2007).

Climate warming has been observed to shift timings in plant phenologies. In a study of 385 British plant species, 16% flowered earlier than previously with only 3% having delayed flowering (Angilletta 2009). The early flowering of several spring plants caused by an abnormally warm spring in northern Japan affected a mismatch in phenologies between the plants and their bee pollinators resulting in a decreased seed yield for that season (Yang and Rudolf 2010). It has been predicted that by the end of the 21st century plant and pollinator phenologies will advance between 1 and 3 weeks, and display significant variation between individual species (Memmott *et al.* 2007).

Shifts in timing of breeding have been observed across a number of taxa, including birds, insects, mammals and amphibians, in response to climate change (Parmesan 2006; Primack *et al.* 2009). Egg-laying dates for Northern hemisphere birds were observed to have advanced by 3.70 days/decade ±0.3 (n=41 species), and have been attributed to an increase in spring temperatures (Parmesan 2007). However, wide intraspecific variation has been observed because species' populations are responding to localised as opposed to global rates of warming , for example, species of birds, from the same continent, were observed to show variation in timing of egg laying due to the seasonal variation in the degree of warming they experienced just before breeding (Angilletta 2009).

There are also many studies which show that migratory species are arriving earlier (Root *et al.* 2003). Migratory species respond to annual seasonal cues, such as day-length and temperature (Primack *et al.* 2009), thus their behaviours, including migratory routes are sensitive to changes in the timing of these cues caused by climate warming (Fischlin *et al.* 2007). For example the Sooty Shearwater (*Puffinus griseus*), a pole to pole migrant, was observed to shift its migratory route by hundreds of kilometres in relation to changes in the sea surface temperature of the Pacific (Parmesan 2006). The fact that many species will breed at one location before migrating to another area to spend the nonbreeding period means that there is an inherent risk in such change in migratory strategy (Fischlin *et al.* 2007). Migratory species are predicted to be more vulnerable to climate change than permanent residents because of the heightened risk of asynchrony between species and resources (Fischlin *et al.* 2007). This is particularly relevant in relation to food availability, where many species may experience detrimental shortages due to mismatches in their phenologies with their food species (Root *et al.* 2003). For example, changes in timing and route of migration of African ungulate species could critically affect the predators which rely on their passing (Fischlin *et al.* 2007).

Individuals can adapt to rapid environmental change by adjusting their rate of development, either by acceleration or deceleration (Yang and Rudolf 2010). For instance most insects are able to grow quicker and mediate shorter generation times under higher environmental temperatures (Berg *et al.* 2010). There is however an optimal increase in temperature, beyond which the effect of increased temperature becomes deleterious (Thomas *et al.* 2004).

Changes in phenological timings can be attributed to changes in a number of different environmental factors; many life-history events are triggered by temperature-related cues, such as seasonal temperatures, Walther et al. (2002) reported that spring timings of activities have been getting progressively earlier since the 1960s, due to warmer spring temperatures being the equivalent of suitable conditions that previously occurred later in the season. However, others rely on day-length or food availability at stop-over points, and some rely on a combination of environmental cues (Parmesan 2006; Primack *et al.* 2009). For example, changing snow patterns in Colorado, USA, have been observed disrupting animal movements, and resulting in increased mortalities (Fischlin *et al.* 2007). Regional differences in warming can explain the variance in advancement of vernal activities found across different locations, for example where differences are observed for Northern and Southern hemisphere species (Angilletta 2009). However, there is also evidence of more localised phenomena in shifting timings that between urban environments compared to rural ones. This is caused by the urban heat island effect which has an additive effect on temperature and is a key cause of greater advancements in phenology in cities (Angilletta 2009). Those species which are unable to respond to climate change by shifting their phenologies may be disproportionately negatively impacted, particularly those residing in highly seasonal environments (Both *et al.* 2010).

Where climate change is considered the driving force in altering Species phenologies, different species are likely to react to different parameters of climate change (Walther 2010). When species that closely interact or compete display divergent responses or vulnerabilities to environmental change, the outcome of their interactions is likely to be altered (Walther *et al.* 2002), mediating not only community structural changes, but also species interactions such as competition, predator–prey relationships, parasitic infections and the decoupling of mutualisms (Williams *et al.* 2008). Both *et al.* (2009) describe the impact of phenological changes in a simplified food chain across four trophic levels in a northwest European deciduous forest. They found that across the four species (representing the trophic levels) studied each shifted their phenologies to different magnitudes exposing asynchronies across the ecological network.

As shifts in range and phenology continue to be played out in this period of climate change some ecological interactions have become uncoupled, as some species move faster or directionally opposite to the species with which they share an interspecific relationship (Angilletta 2009). Ecosystem communities display 'rivet-like' thresholds (Ehrlich and Ehrlich 1981) beyond which they display acute sensitivity to elimination of highly connected species (Dunne *et al.* 2002). The 'rivet' model likens the loss of species to that of the loss of rivets on a plane wing. The loss of one 'rivet' will not cause the wing to break, with relation to species because several roles overlap across species ecosystem processes will be maintained with the loss of a single species. However, there is a threshold beyond which the loss of further 'rivets' will result in the breakdown of the system (Ehrlich and Ehrlich 1981). This alteration in interactions between species has the potential to have as great, if not greater, impact on ecosystems as the impacts of direct abiotic climate change (Yang and Rudolf 2010).

2.2.2 Changes in species range, abundance and extinction

Range Shifts: Observed species range shifts

Evidence that species and ecosystems are sensitive to small perturbations in global mean temperature increases are widespread (Leemans and Eickhout 2004). There is general agreement that climatic regimes influence species' distributions (Walther *et al.* 2002). Parmesan & Yohe (2003) reported that of 80% of species (n=434) undergoing shifts over the past 17-1000 years did so. The paleoecological record reveals that past millennia distributions have fluctuated between range expansion and contraction as species experienced glacial cycling (Walther *et al.* 2002). Past fluctuations in temperature and precipitation have influenced the shape of current distributions by altering habitat suitability across the landscape in which the species reside (Walther *et* *al.* 2002). A species' ability to disperse across the landscape is also constrained by species- specific physiological thresholds (Walther *et al.* 2002).

Over the past decades terrestrial species distributions have been largely observed to shift poleward, and upward in elevation, in correlation with the direction of warming (Parmesan 2006). However, a species ability to shift its range in response to climate warming is constrained by associated changes in climatic factors such as precipitation, non-climatic factors such as land-use and multi-species interactions (Chen *et al.* 2011). Thus, species have also been observed moving away from the poles and downhill due to the interactive features of climate with these factors (Sunday *et al.* 2012).

Parmesan & Yohe (2003) performed a meta-analysis across observed species shifts and reported range shifts averaging 6.1km per decade, a rate much faster than one would expect in terrestrial ecosystems (van Vliet and Leemans, et al 2006). The maximum range shifts, found for the most vagile species, vary from 200km per decade, for butterflies, to a 1000km per decade for marine copepods (Parmesan and Yohe 2003). Sedentary species such as tree species are shifting at a much slower rate as populations undergo extinction and colonisation events (Walther *et al.* 2002). For instance, trees in Sweden exhibited a 30 year lag-time between climate shifts and dispersal of seedlings beyond the current tree line (Parmesan 2006). Large variation has been observed in dispersal capacity across and within taxa, this fact is thus reflected in the large variation in their ability to track climate change through range shifts (Chen *et al.* 2011). The rate and range of dispersal has shown itself to be very idiosyncratic with broad differences both within and among taxonomic groups (Parmesan 2006). Dispersal capacity is also likely to be determined by whether a species is generalist or specialist (Berg *et al.* 2010). Generalist dispersal is less likely to become resource-restricted whereas specialists are reliant on interactions with prey or host species so their dispersal is likely to constrained by the dispersal of the species upon which they are reliant (Berg *et al.* 2010).

Recent observations have shown that species' responses to climate change are most pronounced at the species range ecotone, the edge of the species' range (Parmesan 2005). Climate-induced changes have also been observed to be more marked at the 'leading edge' than the 'trailing edge' with observed colonization rates at the 'leading edge' perceived to be higher than associated local extinctions at the 'trailing edge' (Chen *et al.* 2011; Sunday *et al.* 2012). Range shifts also have tended to be episodic, rather than monotonic or gradual, occurring in stages as regions become climatically viable for dispersal (Walther *et al.* 2002).

Regional, highly spatially heterogeneous, temperature changes are more salient for populations, assemblages, and ecosystems (Walther *et al.* 2005). A meta-analysis of recent species ranges shifts found that species moved at rates more attuned with localised temperature changes, than global rates of warming (Chen *et al.* 2011). The finding that shifts in precipitation have often diverged from those observed for temperature, occurring in different geographical directions (Dobrowski *et al.* 2013), brings added complexity to the picture. This climate complexity complicates the identification of an overriding pattern and direction of change in species' range shifts.

Future projected range shifts

Range shifts are likely to be the primary response of most species to climate change (Parmesan 2006), with more species likely to shift to new different patches than remain and adapt in their own patch (de Mazancourt *et al.* 2008). Species' distributions are likely to exhibit one of two trends, i) range expansion because previously uninhabitable regions open up to colonisations and, ii) changing climates will force contraction in range size, as species can no longer operate within that climate zone. This will largely depend on species' adaptations and their specific environmental tolerances (Stewart *et al.* 2010). Species are unlikely to shift synchronously resulting in fluctuating dominances of species within communities (Walther 2010).

Projections of future species' ranges are often generated using one of two modelling methods, i) the correlative ecological niche models, which estimate future ranges based on a species current distribution and climate, and ii) mechanistic process-based models which use species' life history processes and dynamics to predict future ranges (Guisan and Zimmermann 2000).

In estimating a species' ability to track climate change by dispersal it is important to quantify the likely velocity of future climate change and the probable dispersal capacity rates achievable across landscapes. Several studies have estimated the velocity of climate change expected to occur into the next century, and have included projections for various aspects of climatic change including temperature and precipitation velocity (Loarie *et al.* 2009; Sandel *et al.* 2011; Dobrowski *et al.* 2013). These studies measure the rate of climate displacement across the landscape, based on estimates of past velocity and projections of future climate velocity, giving a valuable indication of the rate of dispersal a species would need to achieve to keep pace with climate change. Species are known to have experienced climatic changes throughout their evolutionary history, however, in past millennia the rate of change was at a slower pace (Root *et al.* 2003). Where species' dispersal capacity exceeds predicted rates of climate velocity, species are projected to be able to track climate changes (Sandel *et al.* 2011).

Under the IPCC SRES A1B scenario, which represents intermediate climate warming, Loarie *et al* (2009) predicted a geometric mean velocity of 0.42km/yr change in temperature with an associated range of 0.11-1.46km/yr for the period 2000AD to 2100AD. The projected rate is dependent on the emission scenario used and the period of time over which it is calculated. However, Loarie *et al* (2009) reported that patterns of global velocity change appeared in parallel across the scenarios tested, with the highest climate change velocities occurring in flat landscapes at higher latitudes.

Temperature gradients differ across the globe, thus the actual climate change velocities experienced by individual species are subject to high variation in part due to differences in regional rates of climate change, but also the degree of altitudinal relief (Loarie *et al.* 2009). Therefore patterns of expected range shifts for species will differ across the globe in keeping with different regional levels of warming (Chen *et al.* 2011). For example, species in mountainous biomes will require the slowest dispersal rates to keep pace with climate change, whereas those species in flatter biomes, such as desert, mangroves and flooded grasslands are projected to require much higher dispersal velocities (Loarie *et al.* 2009).

At a local spatial and temporal scale climate is less dominant in defining species distributions than differences in topology and geography such as terrain, soil type and hydrology (Leemans and Eickhout 2004). Thus, predicted climate space may be uninhabitable because the underlying geology and flora is incompatible for the species (Lanchbery et al 2006). For example a shift from non-forest to forest can negatively affect those species which are adapted to treeless conditions. (Scholze *et al.* 2006).

The degree to which a population is isolated will also influence the degree to which species are able to persist within the landscape, for example terrestrial species may be dispersal limited because they inhabit islands or mountain ranges (Lanchbery *et al.* 2006). Any increase in the mean distance between natural habitats further compromises the ability of species to successfully disperse between populations and habitat patches (Parmesan *et al.* 2000). Natural physical barriers such as mountain ranges, water expanses i.e. ocean and rivers and barren landscapes, will also limit species' abilities to disperse to future climatically suitable regions (Lanchbery *et al.* 2006).

There is high variation across taxa in their ability to disperse (Guisan *et al.* 2006; Midgley *et al.* 2006). Rapid changes in climate zones are likely to further enhance the risk of extinction for those species with a low capacity for dispersal and subsequent colonization (Williams, Jackson and Kutzbacht 2007). Temperature change is likely to be a major factor in determining geographical range, however some tree species may not be able to disperse and keep pace with changing temperature zones (Fischlin *et al.* 2007). The maximum dispersal rate of common tree species is estimated at less than 100km per century (Leemans and Eickhout 2004) too slow to keep pace with the current rate of change.

The modern landscape holds little inherent capacity for ecosystems to adapt under rapid environmental changes (Walther *et al.* 2005). Human-mediated stressors such as habitat fragmentation and land use changes are likely to reduce many species' ability to disperse through the landscape(Thomas *et al.* 2004; Lanchbery *et al.* 2006; Wiens *et al.* 2009). Climatically suitable locations may be remote from species current distributions and occurring beyond species' dispersal capacities which are significantly reduced by habitat loss and fragmentation (Walther *et al.* 2005; Williams, Jackson and Kutzbacht 2007). Species movement is also likely to be moderated by processes such as competition, herbivory and soil formation (Fischlin *et al.* 2007) . Humans can also enhance the ability of species to track climate change, purposefully or unintentionally. Translocation (the movement of species within their historic range) and assisted migration (relocating the species beyond its historic range), are two processes intended to aid species dispersal.

These species are likely to experience large range contractions as suitable climate space shifts beyond their dispersal capacity (Ashcroft 2010). Shrinking habitat availability is predicted to cause a number of species to retreat into refugia, areas of habitat in which species can persist during unfavourable climate regimes (Ashcroft 2010). Those species which preferentially inhabit cooler conditions currently are most at risk of large range contractions, as their current distribution may already be restricted to interglacial refugia, and any further rise in temperature will compromise their ability to survive further (Ashcroft 2010). Warm-adapted species which have undergone range expansion during the current interglacial may, in time, also suffer range contractions, as warming surpasses their upper tolerance limits (Ashcroft 2010).

Mountains are becoming increasingly important as refuges for species, particularly endemics (Fischlin *et al.* 2007). However, montane species occurring on mountain tops are disproportionately sensitive to climate change because they cannot move further upwards as warmer thermoclines transition to higher elevations (Parmesan 2005; Thuiller *et al.* 2006). As natural ecosystems become smaller and further isolated and populations go into decline they are less able to adapt particularly when faced with the increased occurrences of disturbance events (Parmesan *et al.* 2000). Species responses to the disappearance of their climate niche and the appearance of novel climates in their sted are difficult to predict (Williams and Jackson 2007). Thus, forecasting the effect of unfavourable climates on biodiversity and ecosystem services is highly complex because it requires us to extrapolate beyond what is known (Williams and Jackson 2007).

Abundance

Changes in abundance are implicated in observations of range shifts, where recent climate change has either enhanced or reduced the amount of available climate space for species and resulted in colonisation opportunities or localised extinctions (Chen *et al.* 2011). Abundance changes are measured by changes in population size for individual species, or shifts in community structure and have been associated with 1) individual species physiological tolerance limits (Parmesan *et al.* 2000) and, 2) changes in community composition which have created multiple disconnects in species interactions (Cahill *et al.* 2013). Identifying concrete examples of species abundance changes caused by climate change is complicated by the interaction of confounding factors such as land-use changes, competition from invasive species and disease (Cahill *et al.* 2013).

Examples of abundance changes related to physiological tolerance limits directly are rare for terrestrial animals (Cahill, 2013). However, warming, at least in a regional context, has been cited as the causative factor in several catastrophic population die-offs (Portner and Knust 2007; Welbergen *et al.* 2008; McKechnie and Wolf 2010). For example, recent increases in severe heat waves in hot desert regions have led to mass avian mortalities, in 2009 Western Australia experienced a heat wave which caused the death of thousands of birds unable to successfully thermoregulate. These die-offs will periodically reduce populations increasing their vulnerability to further extreme events (McKechnie and Wolf 2010). Ziegeweid et al. (2008) found that shortnose Sturgeon (*Acipenser brevirostrum)* populations are in decline*,* because increased summer water temperatures are lethal to their young, leading to a decline in juvenile recruitment. In Polar Regions, where temperatures are increasing at the greatest rate, polar species' populations tend to be marginally stable or in decline, as their climatically suitable habitat shrinks, whereas temperate species at the same site are increasing in abundance (Parmesan and Yohe 2003). For some species an increase in average global temperatures may boost their reproductive success by creating suitable conditions for unusually high reproduction with the result of increased abundance (Zimmermann *et al.* 2009).

There are some species, mainly reptiles, for which temperature plays a role in determining the gender balance of their constituent populations, known as environmental sex determination (Freedberg, Ewert & Nelson., 2001). There is evidence that climate change has already impacted sex ratios by way of increases in average temperatures and the frequency of extreme temperature events, with the potential to impact on their abundance as a result of highly skewed population sex ratios (Parmesan *et al.* 2000).

When species that closely interact or compete display divergent responses or vulnerabilities to environmental change, the outcome of their interactions is likely to be altered (Walther *et al.* 2002). Declines in abundance and local extinctions due to disconnects in species interactions are equally difficult to identify, however, Cahill et al (2013) give several examples of this phenomena. These include the local extinction of desert bighorn sheep (*Ovis canadensis*) in California caused by a reduction in food availability, as lowered rainfall in the region altered the plant community on which it relied (Cahill et al, 2013).

One observed indirect impact of recent climate change, the measureable rise in incidence and spread of wildlife diseases, parasites and zoonoses is likely to further compromise already vulnerable species (Fischlin et al., 2007). The impact of this measured rise in pathogens has already been implicated in the widespread extinction of amphibians (Pounds et al. 2006).

Reductions in abundance are likely to severely impact genetic diversity, causing evolutionary shifts as the gene pool shrinks (Williams et al, 2008). The degree to which genetic diversity is lost will be dependent on the ability of a species to migrate and the amount of range contraction (Williams et al, 2008).

Extinction

Observed global extinctions

There is relatively little evidence of extinctions caused by recent climate change but studies suggest that rates of future extinction due to climate change could surpass those caused by habitat destruction in the next decades (Bellard *et al.* 2012). The fossil record shows that extinctions have accompanied periods of past global climate change (Fischlin *et al.* 2007). Thus, the likelihood of extinctions occurring with future climate change is high, particularly considering that the climate is likely to be warmer than during any point in the last 1-40myr (Thomas *et al.* 2004). A predicted rise of 2°C rise in temperatures from pre-industrial levels will significantly compromise many species, particularly endemics, putting them at a far greater risk of extinction (Fischlin *et al.* 2007).

The IUCN has attributed climate change as a significant factor in the extinction or extinction in the wild of 20 species out of 864 recent extinctions, representing seven amphibians, six birds, four molluscs, two fish and one mammal (Cahill *et al.* 2013). However, the links with climate change are tenuous, as each of the specie's populations was already compromised by non-climate factors (Cahill *et al.* 2013). Although global extinctions are difficult to attribute to climate change, there is clear evidence that localised extinctions are occurring and are especially prevalent at the warm edge of species' ranges (Cahill *et al.* 2013).

In a recent review on localised extinctions encompassing 136 studies, Cahill *et al* (2013), discovered that very few were found to be the result of changing temperatures directly, and attributed causes also included the disruption of species interactions, precipitation changes and an increase in disease incidence. For example, recent amphibian extinctions have been attributed to warming which indirectly created optimum conditions for the spread of the fatal *Batrachochytrium* fungus (Fischlin *et al.* 2007).

Future projected species extinctions

Species extinctions have been forecast across the world's ecosystems as a result of climate change. Model predictions of species' responses to climate change, in particular changes to their natural ranges, predict that with a small degree of further warming, species extinctions are likely (Lanchbery et al 2006). Projections of future global extinctions estimate that 20-30% of species experiencing 2-3°C warming above pre-industrial levels; will be increasingly at risk of extinction (Fischlin *et al.* 2007). Large variation among regional biota means that this extinction figure may be as low as 1% and as high as 80% (Fischlin *et al.* 2007).

Extinctions and local extinctions or extirpations are predicted to especially prevalent among range-restricted or isolated species and populations (Fischlin *et al.* 2007). As such, climate change is predicted to disproportionately affect endemic species; Thomas *et al* (2004) predicted that by 2050 between 15-37% of endemics will be committed to extinction. Thomas *et al*'s interpretation of what constitutes an endemic is broad and defines endemic species as those confined to one region i.e. the whole of Europe. Isolated islands with high numbers of endemic species, such as the Galapagos Islands and Madagascar, are predisposed to experience high extinction rates (Vamosi and Vamosi 2008). The same is true for biodiversity hotspots, which are predicted to experience high rates of extinction simply due to the number of species they harbour (Pimm and Raven 2000). In the South African Succulent Karoo biome, 2,800 plant species face potential extinction as bioclimatically suitable habitat is reduced by 80% with a global warming of 1.5-2.7°C (Fischlin *et al.* 2007).

Species expected be most at risk of extinction are those inhabiting mountain ecosystems, particularly montane tropical forests (Fischlin *et al.* 2007), and species which have already been exposed to other stressors, such as habitat loss (Williams and Jackson 2007; Williams, Jackson and Kutzbacht 2007). Climate change is predicted to supersede land-use change as the dominant driver of biodiversity loss beyond 2050 (Fischlin *et al.* 2007).

The response of individual species to altered conditions will instigate a cascade of effects throughout the ecological network (Walther 2010). If key species, (i.e. those species with many connections within the food web structure), move out of the system or go extinct, there is a high likelihood that a wave of secondary extinctions will follow (Dunne *et al.* 2002). The loss of basal species, such as primary producers, which form the foundation of food webs, or the loss of key prey for a specialized predator that itself is predated, are both triggers for extinction cascades (Dunne *et al.* 2002). The more highly diverse communities, with high numbers of endemic species (i.e. tropical communities), are more vulnerable to change as they are dependent on complex sets of interspecific interactions (Vamosi and Vamosi 2008).

Over the next 100 years the major proximate factors attributed to extinctions are likely to vary in response to further climate change, with the likelihood that species extinctions caused by physiological limitations will increase as warming continues (Cahill *et al.* 2013). At the current time there is little information available on time lags between the occurrence of a climatic signal and subsequent species extinctions, and it could be many decades before the full impact of environmental disturbance is manifested as extinctions (Thomas *et al.* 2004).

Climate change will further aggravate the stress which many species are already experiencing due to a multitude of stressors, such as habitat loss and fragmentation caused by land-use change (Fischlin *et al.* 2007). Approximately 60% of all world ecosystems evaluated are unsustainably exploited and as a result they are increasingly being degraded (Fischlin *et al.* 2007). Around 20% of all mammal species, 30% of amphibians, 21% of reptiles and 13% of bird species are currently recognised as threated (critically endangered to vulnerable) in the IUCN red list (IUCN 2013). The additive impact of climate change has the potential to consign these already threatened species to extinction by further compromising their ability to survive (Fischlin *et al.* 2007).

The complexity associated with modelling climate change associated extinctions, lies not only the additive effects of other detrimental drivers (Leuzinger *et al.* 2011) but also with the coarse spatial scale over which these predictions are made (Willis and Bhagwat 2009). This large spatial scale fails to account for 'microclimatic buffering", misses potentially important topographical features, and doesn't account for individual species ability to acclimate to changing climates(Willis and Bhagwat 2009). However, bioclimatic envelope models are the best tool available for making widespread predictions of extinction risk, particularly for species for which we have little information.

2.3 Adaptation and its limits

The physical impact of climate change on species will depend on the ability of species to utilise those innate adaptive responses such as acclimation, adaptation, dispersal and behavioural changes (Bellard *et al.* 2012). This innate adaptive capacity, termed autonomous adaptation, consists of a suite of adaptation options which can be separated into three main categories; Ecological, Phenotypic and Genetic adaptations (Williams *et al.* 2008). These function at different temporal and spatial scales and operate from the level of the individual, to population and system wide (Smit and Wandel 2006). For adaptive responses to be successful in responding to rapid climatic change three criteria need to be fulfilled; 1) that the quality of habitat connectivity in the landscape is good, 2) that the species and systems adaptive mechanism are able to keep pace with the velocity of climate change, and 3) that there is sufficient genetic variability within populations and systems (Williams *et al.* 2009). Species biological limits will limit the degree to which species can adapt to climate change (Williams *et al.* 2008). For example, ectotherms body temperatures are determined by external heat sources (Cossins and Bowler 1987), temperatures beyond their thermal tolerances will compromise these species ability to adapt (Deutsch *et al.* 2008). Those species which have low adaptive capacity and/ or dispersal ability are likely to be caught in a dichotomy, as climate-forced range changes impact and they struggle to disperse to suitable climates, ultimately making them more vulnerable to extinction (Walther *et al.* 2002). Therefore species have two paths, either 'survive in situ in small refugia or be sufficiently generalist to utilize a broad habitat mosaic containing a matrix of suboptimal habitat types' (Williams *et al.* 2009). Those species with limited autonomous adaptive capacity are likely to require human-intervention to survive.

2.3.1 **Species and Ecosystems Adaptation Pathways**

The degree to which species will survive or an ecosystem will persist under climate change will depend on each one's capacity to adapt as well as their respective innate resilience (Williams *et al.* 2008). Resilience refers to the amount of disturbance a system or species can tolerate and recover from (Gunderson 2000; Williams *et al.* 2008). The fact that ecosystems are dynamic entities, able to exist in alternative stable states, points to their innate capacity for autonomous adaptation, at least within the bounds of previously experienced variability (Gunderson 2000). There is also a wealth of evidence to suggest that species have also undergone adaptation during past climate cycles (Parmesan 2006). However, this evidence of past adaptation does not necessarily indicate that ecosystems and species will be able to adapt to novel conditions (Willis *et al.* 2009).

There is evidence that species have already used pre-existing flexibilities in responding to climate change, such as contraction to refugia, shifts in distribution, and shifts in habitat and microhabitat, shifts in seasonal and daily activities, acclimation, and changes in biotic interactions (Williams *et al.* 2008; Wiens *et al.* 2009). These responses indicate that species are able to act within a generation, as opposed to evolutionary genetic changes which will only take affect after multiple generations (Williams *et al.* 2008). These adaptive responses may occur on relatively short time scales due to the pressure exerted by rapid climate change on traits important for persistence (Gienapp *et al.* 2008).

Ecological adaptations include changes in species distributions and phenological adjustments but also individual-based modifications of behaviour, physiology and morphology (Chevin *et al.* 2010). Adaptations can occur both over the short term, from days to weeks, as in the instance of behavioural changes, and the long term in the case of genetic adaptations, and can be reversible, semi-permanent and permanent (Helmuth *et al.* 2005). As climate change intensifies it is likely to impose strong selection on species' traits which are important for fitness, eliciting phenotypic responses (Gienapp *et al.* 2008). Most observable ecological adaptations are governed by phenotypic plasticity, changes in abundance and distributions being the notable exceptions (Helmuth *et al.* 2005).

A species' or individual's sensitivity to environmental change is governed by intrinsic factors which include their physiological tolerance limits, their ecological traits such as behaviour, and their inherent genetic diversity (Williams *et al.* 2008). Species that are especially vulnerable to rapid environmental change are those that are genetically-poorly adapted to their environments, reproduce slowly, cannot disperse effectively, and are highly specialised or isolated, because they are highly sensitive to environmental change (Fischlin *et al.* 2007). The extent to which a species is able to adapt is often constrained by its evolutionary history; this is particularly salient in the case of generalist versus specialist. Generalists will more readily adapt to changes in climate, whereas the nature of specialization means that specialist's adaptive capacity is restricted. However, specialist species may inherently be more resilient to localised change due to the demographic advantage of high and uniform local abundance, localised adaptations and a higher capacity to disperse across their suitable habitat due to local adaptations (Williams *et al.* 2008; VanDerWal, Shoo, Johnson, *et al.* 2009). A species' sensitivity and thus its vulnerability are dependent on the level of exposure to climate change but determined by the species resilience and adaptive capacity (Williams *et al.* 2008).

It is argued that environmental change is inclined towards selecting changes in species abundances and distributions as opposed to phenotypic adaptations (de Mazancourt *et al.* 2008). With increasing rates of change a species ability to adapt declines rapidly (Leemans and Eickhout 2004). Leemans & Eickhout (2004) predict that with between 1 and 2°C warming most species, ecosystems and landscapes will have experienced a degree of climate change which will severely limit their adaptive capacity, manifesting in observable biodiversity declines. There is a general lack of information regarding most organisms physiological tolerances and intrinsic genetic diversity (Hoegh-Guldberg *et al.* 2008). However, tolerance limits are thought to be phylogenetically constrained meaning that a representative species may be appropriate to describe the taxa (Hoegh-Guldberg *et al.* 2008)

Phenological and Physiological

Species adaptations in phenological and physiological characteristics are controlled by phenotypic and genetic variation within populations. Phenotypic variation describes the range of observable characteristics or traits which a species can employ in adapting to environmental change. These traits include morphological, developmental, phenological and behavioural traits. The inherent phenotypic variation which currently exists among individuals across populations has been produced across countless generations in response to previous climatic fluctuations (Angilletta 2009). Often there are multiple phenotypes present within a population (Helmuth *et al.* 2005). Variation in the rates and degrees of expression of each variation during past periods of environmental change will determine how prevalent each phenotype is among the population (Helmuth *et al.* 2005). Phenotypic plasticity can operate in the short-term and does not require multiple generations to elapse before being expressed, as in genetic adaptation (Williams *et al.* 2008)

Phenotypic plasticity is itself dependent on the level of intrinsic genetic variation of the species in question (Williams *et al.* 2008). However, the phenotypes of organisms can adjust in direct response, to environmental change without the need for genetic adaptions (Thomas 2005). Certain life history traits are thought to support resilience these include a short life span, high reproductive capacity and fast life history (Williams *et al.* 2008). The most vulnerable species include those that are genetically poorly adapted to rapid change, disperse poorly, reproduce slowly, are isolated or highly specialised (Fischlin *et al.* 2007). However, some of the most profound effects of climate change species are expected to encounter are likely to be related to the decoupling of biotic interactions among species (Parmesan 2006; Yang and Rudolf 2010).

There is not infinite variation in phenotypic plastic responses, they are physiologically limited and likely to 'saturate' under extreme environments (Chevin *et al.* 2010). For example, metabolic rates cannot increase or decrease *ad infinitum* under persistent environmental change (Chevin *et al.* 2010). A sustained rise in experienced mean temperature, as is predicted with climate change will test species ability to function, by pushing species closer to, or beyond their critical thermal limits beyond which species life processes are unable to function (Angilletta 2009). The thermal sensitivity of these processes places strict limits on life (Portner and Farrell 2008; Angilletta 2009). Species exploitation of their inherent phenotypic plasticity may imply involve fitness costs to the individuals, associated with the expressed phenotype or otherwise (Chevin *et al.* 2010). Large phenotypic plasticity does not, however, foretell a high degree of genetic variation (Thomas 2005).

It is important to consider the full breadth of phenological and physiological adaptations to climate change in particular, increases in temperature, if we want to predict species responses to climate change (Franklin and Seebacher 2009).

Phenological

There is inherent flexibility in many species phenological activities, this flexibility means that these species are able to modify the onset and cessation of specific annual activities to adapt with climate change (Kearney and Porter 2009). This phenotypic plasticity means that these species can remain in synchrony with changing seasonal conditions without having to evolve genetic solutions (Kearney and Porter 2009). However, predicting the adaptation of species phenologies to climate change is complicated by the complex nature and multi-layered character of environmental cues on which species rely to prompt the onset of phenological activities (Walther *et al.* 2002; Parmesan 2006; Primack *et al.* 2009). There is inherent risk associated with changing strategy, in terms of mismatches between predator arrival and prey availability, or breeding during a short-term warm period which then reverts back to a cold period resulting in mortality of vulnerable juveniles unable to withstand cool temperatures (Primack *et al.* 2009). The asynchronous timing of phenological events among community members has the potential to negatively disrupt ecosystem functioning, making the community more vulnerable to climate change (Primack *et al.* 2009). The evidence for, and predicted effect of climate change on phenologies is reviewed in section 2.2.1.

Physiological

Physiological adaptations occur at the individual mechanistic level exploiting intrinsic phenotypic plasticity, or genetic variability. Phenotypic plasticity can be employed rapidly but has limited scope, whereas genetically- based adaptations act over a longer timescale but are less constrained (Williams *et al.* 2008).

A physiologically-based example of phenotypic adaptation is acclimatisation. This is the process by which endotherms are able to make seasonal phenotypic adaptations to their insulative properties and metabolic processes (Angilletta 2009). This process allows organisms to respond rapidly to warming (Angilletta 2009), it is a short-term phenotypic adaptation (Deutsch *et al.* 2008) to temporary environmental change and involves the compensatory adjustment of physiological function to increase the individual's resilience (Helmuth 2005). Acclimatory responses are induced by environmental stimuli, and are reversible over the species' lifetime; as such these adaptations are not passed onto the next generation (Cossins 1987). Acclimatisation, although a phenotypic adaptation, is limited by the individual's genotypic variation (Cossins 1987). The ability for a species to acclimatize is dependent on their intrinsic thermal tolerances which are proportional to the temperature variation they have experienced over their lifetime, although this variability is also constrained by the latitude of their location (Deutsch 2008). As such, individuals with a greater resistance to thermal stress are conferred a selective advantage in evolutionary terms (Cossins and Bowler 1987). However, species with high tolerances to extreme temperatures may be at a disadvantage under non-stressful thermal environmental conditions because of the large cost associated with immediate plastic responses (Williams *et al.* 2008).

It is likely that some species will adapt their morphology (Root *et al.* 2003) in response to changes in energetic constraints placed on them by climatic change. Energetic constraints are known to influence size and shape but also the colour of individuals (Parmesan *et al.* 2000). As such outward morphological adaptations are mainly an indirect result of adaptations required to better align a species individuals energy budget to a new set of environmental conditions. For example the Scops owls (*Otus scops)* of Italy have adapted to recent warming and increased precipitation by adopting a measurably darker plumage (Galeotti *et al.* 2009).

Behavioural adaptations

Species have the ability to modulate their behaviour in response to climate change, changing patterns in their behaviour rapidly (Kearney *et al.* 2009). Behavioural changes are likely to be the first strategy utilised by species, particularly ectotherms that behaviourally thermoregulate. Moderate warming at a global scale is likely to instigate species to undergo complex behavioural changes at the local scale (Angilletta 2009). Such changes can be a reaction to one extreme weather event or to prolonged climate shifts, and as such, in the short term at least, are reversible (Angilletta 2009). In fact there is mounting evidence that there is a very strong correlation between changes in climate and adaptations in species' behaviour (Lanchbery et al 2006). Species living at high latitudes and altitudes are expected to adapt their behaviours most markedly because these are the regions where the greatest temperature changes will occur (Root *et al.* 2003).

Evolutionary and Genetic

A species' ability to adapt under climate change will depend on a balance between three factors (Williams *et al.* 2008). Firstly, that there is sufficient heritable variation, second, the size of the adapting population (which has indirect effects on evolution) and third, the rate at which climate change is occurring (Williams *et al.* 2008).

Rapid genetic adaptation to new environments has been observed (Dormann *et al.* 2010). This has been especially prevalent among species with short generation times which seem capable of swift evolutionary change (Wiens *et al.* 2009). Conversely, maladaptation to changing climates has been predicted among species with low dispersal capacity and long generation times with the consequence of decreased species' persistence (Bradley St Clair and Howe 2007; Cobben *et al.* 2012). For example, it is predicted that the longevity of the Douglas-fir (*Pseudotsuga menziesii*) will significantly limit its adaptation capacity, as multiple generations over many centuries will be required to adapt to new climate optima (Bradley St Clair and Howe 2007). The risk of maladaptation to climate change was simulated across the range of the middle spotted woodpecker (*Dendrocopos medius*) giving insight into the effect of founder events on species adaptation capacity (Cobben *et al.* 2012). Under increasing temperatures locally-adapted 'specialised' individuals were increasingly marginalised as generalist individuals, better able to adapt to changing temperatures, dominated the expanding range edge (Cobben *et al.* 2012). The loss of specialised individuals had the effect of reducing the gene pool and thus the ability of the species to adapt to further change, causing a reduction in the metapopulation size (Cobben *et al.* 2012).

Species' ability to mobilise genotypic adaptations developed in response to past Pleistocene interglacials and in response to current change has not been determined (Colwell and Rangel 2009). Those species which are dispersal limited and have long generation times, such as forest trees, have the highest probability of undergoing genetic adaptation to local changes in conditions (Bradley St Clair and Howe 2007; Fischlin *et al.* 2007; Chevin *et al.* 2010).

The degree to which species retain genotypic variation which radiated during periods of past climate conditions is unknown (Colwell and Rangel 2009). During the last glacial period, most temperate species occurred at lower latitudes, extending their ranges to higher latitudes as the glacial ice retreated. Thus, most of these species have lower genetic diversity at their northern range boundaries as colonization northward involved few pioneering individuals resulting in new populations containing reduced levels of genetic variation (Thomas 2005). In the Northern hemisphere climate change is disproportionately causing range contractions at the parts of species distributions which hold the greatest genetic diversity (Thomas 2005). The greatest genetic diversity for temperate species is found at the southern most parts of their range. Loss of genetically diverse southern populations and the replacement of populations and colonization of new areas by founder events involving genetically-depauperate northern individuals are reducing the gene pool (Thomas 2005). The bog fritillary, *Proclossiana eunomia,* is one such species threatened by a reduction of genetic diversity. Highly localized remnant populations of the bog fritillary found in the Pyrenees and Cantabrian Mountains of southwest Europe were found to possess four unique alleles (at 10 loci examined) which occur only within these populations (Thomas 2005). The loss of these populations by range contractions will compromise the species ability to adapt to future challenges (Thomas 2005).

Heritability is the proportion of phenotypic variation within populations which can be attributed to genetic variation; most traits exhibited by wild species are heritable, and as such respond to natural selection (Merilä 2012). As a heritable adaptation it represents a permanent shift within the population (Helmuth *et al.* 2005). Genetic responses to environmental change occur when natural selection pressures act on the genetic variability of a population (Frankham *et al.* 2002). Natural selection acts on quantitative traits in a population, selecting for those alleles which confer an advantage in terms of species persistence (Root *et al.* 2003). In this way the population undergoes evolutionary adaptation to align with changing circumstances by selecting for advantageous characteristics over time (Frankham *et al.* 2002). Genetic change can lead to visible change or simply adjustment in physiological activity (Frankham *et al.* 2002). Evolution is most likely to occur when environmental change generates new conditions entirely outside of the range of initial optimal trait values (de Mazancourt *et al.* 2008).

Low levels of heritable variation in traits, specifically tolerance traits, can severely limit a species ability to adapt to climate change (Merilä 2012). It is thought that species distributions may be limited by such genetic variability (Merilä 2012). However, it is important at this stage to consider whether a species current distribution reflects the full ecological potential of the current gene pool or that in fact its current range is constrained by dispersal limitations (Colwell and Rangel 2009).

Evolutionary processes are irreversible within a generation but are reversible if sufficient genetic variation remains dormant within the species gene pool (Frankham *et al.* 2002). Those individual organisms which possess favourable characteristics well-adapted to a particular environment are likely to survive and reproduce better than those less-fit individuals within the population (Cossins and Bowler 1987). Therefore if such favourable characteristics have a genetic basis these beneficial alleles will be driven towards fixation by natural selection (Frankham 2010) over a large number of generations (Cossins and Bowler 1987). As such genetic frequencies in species, at the population level and above are likely to shift in response to climate change (Root *et al.* 2003).

Evolutionary shifts are increasingly probable after population size reductions (Williams *et al.* 2008). Small or reduced population sizes often result in a diminished capacity for local adaptation due to limited genetic variation (Parmesan *et al.* 2000). Across the globe there are untold numbers of recently fragmented populations undergoing genetic erosion, in terms of inbreeding and a loss in genetic diversity, consequently these populations are more vulnerable to environmental change and extinction (Frankham 2010). Such genetic erosion significantly compromises the ability of wild populations to survive (Frankham 2010). Even those species with sufficient genetic variation to adapt to changing climate niches are unlikely to survive unscathed *in situ* because of the rate of evolution required to keep pace with current climate change (Dormann *et al.* 2010). In a study of European mammals, Dormann *et al* (2010) concluded that the studied species would be unable to evolve quick enough to avoid the harmful impacts of climate change.

Genetic factors contribute to a species' overall extinction risk through inbreeding depression, loss of genetic diversity and loss of evolutionary potential (Edmands 2007; Frankham 2010). Predicted species declines are likely to affect the gene pool. As individuals survival ability is compromised a selection-bias toward individuals which can survive perturbations will be incurred, with the potential to result in a genetic bottleneck (Edmands 2007). Loss of genetic variability can lead to an inbreeding depression, the reduction in fitness of a population caused by the mating of close relatives (Edmands 2007). Inbreeding leads to a redistribution of genotype frequencies, reducing heterozygosity, an important factor in maintaining genetic flexibility (Edmands 2007). Populations experiencing stress, such as that imparted by climate change, are approximately 69% more likely to experience an inbreeding depression than under benign environmental conditions (Edmands 2007).

Genetic adaptation is typically a slow process requiring multiple generations to elapse before taking effect; as such it is an on-going dynamical process (Helmuth *et al.* 2005). When the speed of change is rapid in evolutionary terms then species will become maladapted, because genetic adaptation occurs over generations and not within an individual's life time (Donnelly *et al.* 2012). In this way adaptation is a genetic tracking process, which is especially relevant to range-restricted species (Donnelly *et al.* 2012). Thus, it is generally thought that the rapid rate of climate change is too fast for species to adjust evolutionarily, although there is some evidence that changes in genotype are occurring (Wiens *et al.* 2009).

2.3.2 **Human-assisted Adaptation**

Conservation biologist's fundamental tenet is to protect and conserve the earth's biological diversity (Hagerman *et al.* 2010). Global climate change is already significantly impacting biodiversity (Fischlin *et al.* 2007). Therefore, conservationists must aim to maximise the resilience of natural systems to climate change impacts (Mawdsley *et al.* 2009). The major uncertainties associated with climate change, and how to implement novel adaptive management strategies are key challenges (Jackson and Sax 2009; Hagerman *et al.* 2010). Adapting conservation policy to meet these new challenges requires a major paradigm shift and remains a largely unresolved challenge (Araujo *et al.* 2004; Hagerman *et al.* 2010).

Threats to biodiversity fall in to two categories ultimate or proximate (Pressey *et al.* 2007). Ultimate threats operate at a broad scale with political, social or economic roots, for example human population increase and expansion and growth of global markets, as such they are mainly beyond the scope of conservation efforts. Proximate threats directly impact biodiversity and are the expression of ultimate threats at a local scale, for example degradation of an ecosystem by overexploitation of resources.

In a changing world, the object of conservation is to preserve and maintain what are highly complex biological systems for perpetuity (Pressey *et al.* 2007). Within these systems, conservationists seek to retain the ecological, genetic, behavioural, evolutionary and physical processes which are the elements of healthy ecosystem functioning (Bottrill *et al.* 2008). The dilemma now faced by conservationists is whether, with climate change, we should seek to preserve existing assemblages rigidly or whether to allow greater assemblage flexibility and to conserve processes. Dynamic conservation planning will be required to integrate all levels of vulnerability, rates of change and expected changes in biodiversity pattern (Williams *et al.* 2008). To fulfil this need requires identification of those species, habitats and ecosystems most vulnerable, and which aspects of their biology, ecology and evolution make them vulnerable (Williams *et al.* 2008). However, there are still gaps in our knowledge of the relationship between animal diversity, biotic interactions and ecosystem functioning (Chown *et al.* 2004; Hagerman *et al.* 2010). Several strategies have been tabled including; 1) the control of current human stressors and restoration of degraded ecosystems (Williams *et al.* 2008); 2) dynamic management of protected areas (Williams *et al.* 2008), 3) land and watershed management (Pressey *et al.* 2007) and, 4) direct species management i.e. assisted migration and ex-situ conservation (Pressey *et al.* 2007).

Conservation practice focuses on value judgements associated with biodiversity, such as ecological, evolutionary, cultural, social and economic qualities (Bottrill *et al.* 2008). Often the focus is on charismatic species or places, or those species or places perceived to support ecosystems or people (Bottrill *et al.* 2008). A paradigm shift in conservation practice is required to adapt to climate change, conservationists have responded with a series of adaptive conservation strategies and techniques (Hagerman *et al.* 2010). These include, controlling current human stressors and restoration of habitats by reducing land-use change and improving corridors between patches of habitat (Williams *et al* 2008), implementing process-based conservation (Pressey *et al.* 2007) a form of land and watershed management, the dynamic management of biodiversity hotspots (Brooks *et al.* 2002), and direct species management such as focusing on endangered species (Mawdsley *et al.* 2009), conservation triage (Bottrill *et al.* 2008; Hagerman *et al.* 2010) and taxa-based conservation (Hadly *et al.* 2009).

Restoration of Degraded Ecosystems and Reduction in Non-climatic Stressors

The threats to biodiversity brought by climate change are not acting in isolation, they are occurring in concert with habitat loss, pollution, overexploitation, introduction of invasive species and human expansion (Fischlin *et al.* 2007). The challenge for conservation is to identify how, and to some respect when, climate change will interact with these other stressors (Hagerman *et al.* 2010). A primary strategy behind conservation planning for climate change is to reduce stressors which currently undermine ecosystem resilience (Fischlin *et al.* 2007). By controlling and reducing non-climatic stressors, then species and ecosystems will be better placed to react to climate change (Mawdsley *et al.* 2009).

Protected Areas

A key focus of conservation strategy over the past 3-4 decades has been the protection of ecosystems from proximate threats by the establishment of protected areas (Hagerman *et al.* 2010). Significant and rapid range shifts predicted to occur under climate change (Mawdsley *et al.* 2009) mean that current reserve boundaries are likely to be compromised as the protected habitats become unsuitable for those species they sought to protect making previously robust systems sensitive (Araujo *et al.* 2004). Leemans & Eickhout (2004) predict that half of all nature reserves will not be able to meet their original conservation aim, especially as most of them lie in sensitive and exposed biomes. Thus, climate change will create a new class of sensitive areas. Protected area networks are an obvious target for integrating climate adaption policies with strategies designed to combat non-climate stressors.

The current protected area model is inherently spatial (Pressey *et al.* 2007; Hagerman *et al.* 2010), its aim is to achieve ecosystem representation (i.e. a comprehensive collection of all ecosystem types within and across countries) or ecosystem replication, which seeks to conserve several examples of each ecosystem type (Mawdsley *et al.* 2009). Reserves seek to conserve natural features whether they be species, plant communities or landscape types (Cabeza and Moilanen 2001). Fundamental ecological tenets are used to inform protected area location and size. Firstly, based upon the assumption that there is a relationship between species and their location, species are more likely to survive in suitable as opposed to unsuitable habitats (Araujo *et al.* 2004). Secondly, in terms of reserve size and connectivity- large, compact and well-connected reserves are superior to small and isolated reserves, in acknowledgement of the impact of the edge effect and isolation on species persistence (Araujo *et al.* 2004). These rules rely on those characteristics of biodiversity that can be mapped remaining static, and mainly disregards processes that maintain biodiversity (Pressey *et al.* 2007). This practice of ecosystem representation is likely to become obsolete as the distributions and phenologies of individual elements within ecosystems are likely to shift asynchronously resulting in novel assemblages and new ecosystem types (Mawdsley *et al.* 2009).

Under climate change it is possible that a species' entire protected range may disappear; as such one solution could be the expansion or commissioning of new protected areas to represent future habitat structure in the landscape (Pressey *et al.* 2007). Reserve systems need to be designed with long-term shifts in flora and fauna distributions, alterations in natural disturbance regimes and the overall integrity of those protected ecosystems and species, in mind (Fischlin *et al.* 2007). The current time scale over which protected area management is planned is between three and ten years, with reference to planning for climate change, a more appropriate time span would be between 30 and 100 years (Hannah *et al.* 2002). Observed species distributional shifts and phenological asynchronies between species coupled with evidence of ecosystem service disruptions can assist conservationists. For example, creating protected areas which complement observed shifts in species distributions, i.e. along elevational gradients could give these species greater flexibility to shift with climatic change (Hannah *et al.* 2002). Modelling future impacts of climate change on species and ecosystems is one way of informing the planning of future-proof reserves. For example, Araujo *et al* (2004), created a computer model to simulate climate-change induced species extinctions and explored their spatial pattern to inform reserve selection. If extinctions are randomly spaced then spatially dispersed reserves are most likely to protect species, if extinctions are clustered, reserves focused on that region are advisable (Araujo *et al.* 2004). Although current established protected areas may cease to be sustainable in the future they remain to have short term benefits as temporary havens to sensitive species whilst new longer-term refuges are found (Araujo *et al.* 2004; Mawdsley *et al.* 2009). Therefore coordination between established and newly-created protected areas and the wider landscape is crucial to maintain species representation as well as ecosystem processes (Hannah *et al.* 2002).

Landscape Management

For truly dynamic conservation planning conservation practices must move beyond the boundaries of protected areas and become inclusive of the surrounding landscape (Hannah *et al.* 2002). Termed as landscape permeability this technique focuses on enhancing whole landscape connectivity (Mawdsley *et al.* 2009). Maintaining and establishing connectivity between habitat types in the landscape is important in facilitating dispersal and genetic transfer (Williams and Jackson 2007). By encouraging biodiversity friendly land uses, such as agro-forestry, beyond reserve boundaries landscape management seeks to maintain biodiversity in transition (Hannah *et al.* 2002). The need for such measures reflects on the degree to which humans have altered landscapes detrimentally affecting species' ability to migrate in response to climate change (Felton *et al.* 2009). In restoring the surrounding landscape resource managers are able to prepare the terrain if and when species shift (Hannah *et al.* 2002). Landscape management may need to encompass the controlling of disturbance regimes (such as fire frequency) which are likely to be altered by climate change (Hagerman *et al.* 2010). However using disturbance regimes to maintain species beyond their climatic optimum, and suppressing new species colonization as the climate becomes suitable, could be detrimental to ecosystem functioning and biodiversity (Hannah *et al.* 2002). Taking the focus away from individual species management to landscape-wide may negatively impact those species which are rare and have narrow habitat requirement which require a more directed management style (Mawdsley *et al.* 2009).

Assisted migration

Translocation and assisted migration both involve human-assisted movement of species (Mawdsley *et al.* 2009). Translocation involves movement of a species inside its historic range, whereas assisted migration involves relocating the species beyond its historic range. Both techniques seek to relocate species from areas where the habitat is increasingly unsuitable due to climate change to habitats favourable i.e. those within the same broad biogeographic regions, to support their continued existence (Hoegh-Guldberg *et al.* 2008; Mawdsley *et al.* 2009).

Fragmentation of habitats mediated by humans has detrimentally impacted species' potential to disperse across the landscape, this coupled with the expected rate of climate change means there is a distinct possibility that some species will not be able to keep pace climate change (Hoegh-Guldberg *et al.* 2008). Assisted migration could support species with highly fragmented habitats, where connectivity between habitat blocks is disrupted (Hoegh-Guldberg *et al.* 2008). It is also suggested as an option for widespread species that consist of distinct population ecotypes, as the translocation of 'warm-adapted' ecotypes to previously colder parts of the distribution could assist adaptation to climate change (Hoegh-Guldberg *et al.* 2008).

Assisted migration presents many associated difficulties due to the complexity of natural systems and the risk to biodiversity it poses as such its viability as a management option has often been questioned (Hoegh-Guldberg *et al.* 2008; Hagerman *et al.* 2010; Chauvenet *et al.* 2013). Introducing species into novel ecosystems has the potential to create new pest problems through aggressive species colonisations impacting naturalised population genetic structure and breeding systems, but also through the introduction of novel diseases and parasites (Hoegh-Guldberg *et al.* 2008). These risks are thought to be escalated in cases where species are moved across biogeographic boundaries (Hoegh-Guldberg *et al.* 2008). The careful selection of species to undergo assisted migrations may assuage some of these inherent risks (Chauvenet *et al.* 2013), with many conservationists now recommending this expensive and risky option (Fischlin *et al.* 2007; Felton *et al.* 2009).

Ex-situ Conservation

The viability of some wild populations is threatened to the degree that captive populations are established as a form of 'insurance' to prevent species becoming extinct, with the additional impact of climate change conservationists are increasingly likely to consider this option (Mawdsley *et al.* 2009). Example sites of ex-situ conservation include botanic gardens, zoos, seed and gene-banks. One risk of relying on ex-situ conservation to preserve species is that species which no longer have a natural habitat to return to (Mawdsley *et al.* 2009).

Computer Models and Conservation Planning

Advances in the predictive power of computer modelling techniques in exploring the impacts of climate change on ecosystems and species have added another tool to the conservationist's arsenal. Jackson *et al* (2009) state that for conservation measures to succeed our predictive capacity to forecast the course of, and ecological and biological response to, climate change is imperative. Models that make spatially and temporally explicit projections have the potential to be harnessed in the establishment of monitoring programmes, design of future reserve networks and to give information of the expected rate and trajectory of climate change (Midgley *et al.* 2002). These projections need to be based upon our understanding of likely regional climatic and ecological changes if they are to be accurate; therefore monitoring of environmental change and the associated ecosystem responses is tantamount (Fischlin *et al.* 2007). Badly timed interventions, for instance at vulnerable life history stages could make species even more sensitive to climatic change (Jackson *et al.* 2009). There are several types of model available for carrying out such analysis these include global climate models, regional climate models, dynamic and equilibrium vegetation models, species bioclimatic envelope models and site-specific sensitivity analysis models (Hannah *et al.* 2002). These models are often used in synchrony, as ensembles, to determine, for example, the effect of climate change on species distributions, which requires linking global or regional climate models with bioclimatic envelope models (Wiens *et al.* 2009; Jaeschke *et al.* 2012).

3 Calculating Species Sensitivity

3.1 Introducing Vulnerability and Life History Theory

Climate change is predicted to become a major driver of biodiversity loss over the coming century (Thomas *et al.* 2004; Fischlin *et al.* 2007). Four major trends have been observed in terrestrial ecosystems as a result of recent climate change, these are 1) shifts in species' phenology (Walther *et al.* 2002; Parmesan and Yohe 2003), 2) shifts in species' ranges and associated changes in abundance and extinction risk (Walther *et al.* 2002; Root *et al.* 2003), 3) disruption of ecological interactions (Tylianakis *et al.* 2008), and 4) changes in primary productivity. For future conservation the development of measures which improve our predictive capacity to forecast the course of, and ecological and biological response to, climate change is of paramount importance (Chown 2004). Thus, to succeed in predicting future risk will require a combination of knowledge on the degree of threat and of traits which increase species' susceptibility to threat (Fritz *et al.* 2009).

3.1.1 Vulnerability Theory

In striving to aid and improve the assessment of species' vulnerability to future climate change this study employs 'Vulnerability theory' which seeks to account for the many processes and perturbations which influence species' persistence in the environment. Vulnerability is defined by the IPCC in relation to climate change as 'the degree, to which a system is susceptible to, or unable to cope with, adverse effects of climate change, including climate variability and extremes. 'Vulnerability' is a function of three factors, exposure (the character, magnitude, and rate of climate variation to which a system is exposed), sensitivity and adaptive capacity (Adger 2006; Williams *et al.* 2008; Dawson *et al.* 2011). It describes the 'state of susceptibility [of a system or individual] to harm from exposure to stresses associated with environmental [change…]' (Adger 2006; Gallopin 2006). In relation to a species, the term vulnerability refers to the extent to which climate change will introduce a species survival, in terms of declines in abundance, fitness and genetic variation. (Dawson *et al.* 2011). These interactions are explored graphically in the below Venn diagram adapted from Smit and Wandel (2006)(Figure 3.1).

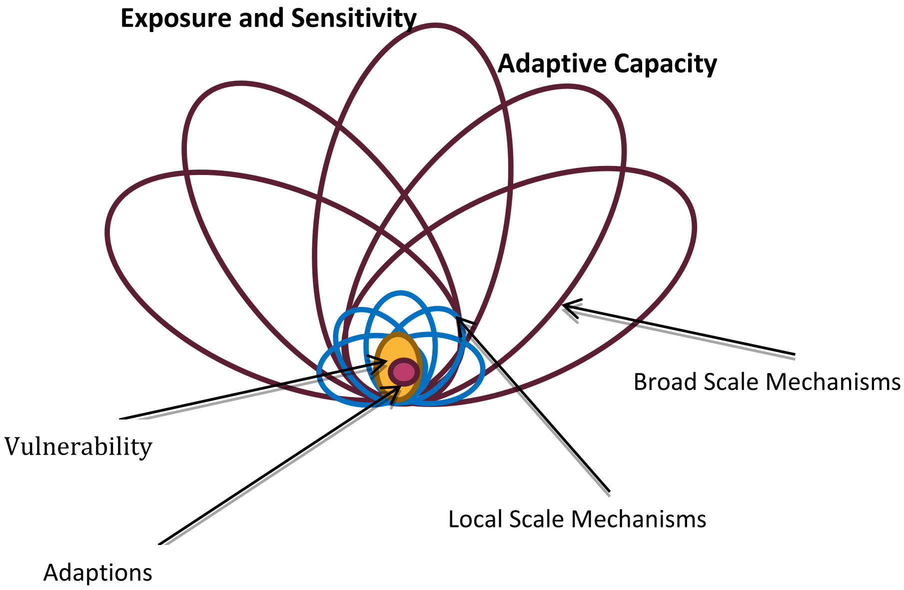


Figure 3.1 Schematic Diagram of Vulnerability Theory (after Smit & Wandel 2006)

The broad scale external dynamics (in purple) determine sensitivity and exposure and inform adaptive capacity at the local or community scale (in blue). These broad scale forces are interactive in determining localised vulnerability, which is itself tempered by intrinsic adaptive capacity (Smit and Wandel 2006). Systems are most vulnerable where they are highly exposed and highly sensitive.

There are several versions of the Vulnerability framework, those which preserve a distinction between Adaptive Capacity and Sensitivity (Chin *et al.* 2010; Summers *et al.* 2012; Berry *et al.* 2013) and those which combine both factors (Williams *et al.* 2008; Foden *et al.* 2013). Those frameworks which preserve the distinction between Sensitivity and Adaptive capacity consider that each encompasses very different attributes, defining ‘sensitivity’ as the degree to which a species is affected by climate change and ‘adaptive capacity’ the potential for of a species to adjust to climate change (Berry *et al.* 2013). Williams *et al* (2008) consider adaptive capacity as a constituent feature of a species overall sensitivity, thus sensitivity is determined by adaptive capacity and species resilience. In this case the theory of vulnerability realised as an equation is:

$$Vulnerability = f(Sensitivity \,\&\, Exposure)$$

Where exposure is the degree to which a species is exposed to future climate change and where Sensitivity is described as the sensitivity of that species to stress. A species' sensitivity is governed by intrinsic traits, and exposure by external factors such as climate change and localised habitat effects (Williams *et al.* 2008). In combining both attributes of 'resilience' and 'adaptive capacity' under the umbrella term 'sensitivity' Williams *et al* (2008) put forward the concept that each component is not mutually exclusive but operate in synchrony to determine a species' response to climate change.

Vulnerability analysis can be viewed as an important framework for the assessment of species' ability to persist under climate change, applicable to both taxonomic and regional species sets (Dawson *et al.* 2011), across timescales (instantaneous to centuries) and mitigation scenarios (Smit and Wandel 2006). Such analysis across species can be used as an indicator to rank species vulnerabilities through the creation of a proxy measure indicating overall Vulnerability through the aggregation of Exposure and Sensitivity scores (Adger 2006; Smit and Wandel 2006). The results of such analysis can be used to inform policy and decision-making in the targeting of resources by identifying in this case taxa or regions are most vulnerable (Smit and Wandel 2006).

The influence of climate change on biodiversity has multiple aspects which need to be accounted for if we are to predict the extent of its influence (Dawson *et al.* 2011). Climate change can be seen as umbrella change representative of many stressors interacting across a range of spatial and temporal scales (Adger 2006). Much research has been focused on the likely impacts of future climate change on species survival. Species distribution models, are one such method which has proliferated, they capitalise on scientific knowledge of biophysical and ecophysiological processes and their regulation of species relationships with their environment (Guisan and Zimmermann 2000; Austin 2007).

These modelled outputs of species range dynamics are best suited to represent exposure, one component of the Vulnerability equation (Dawson *et al.* 2011). To account for the second component of Vulnerability, sensitivity, will require the development of methods complementary to the measure of exposure (Dawson *et al.* 2011).

3.1.2 Aims of the Chapter

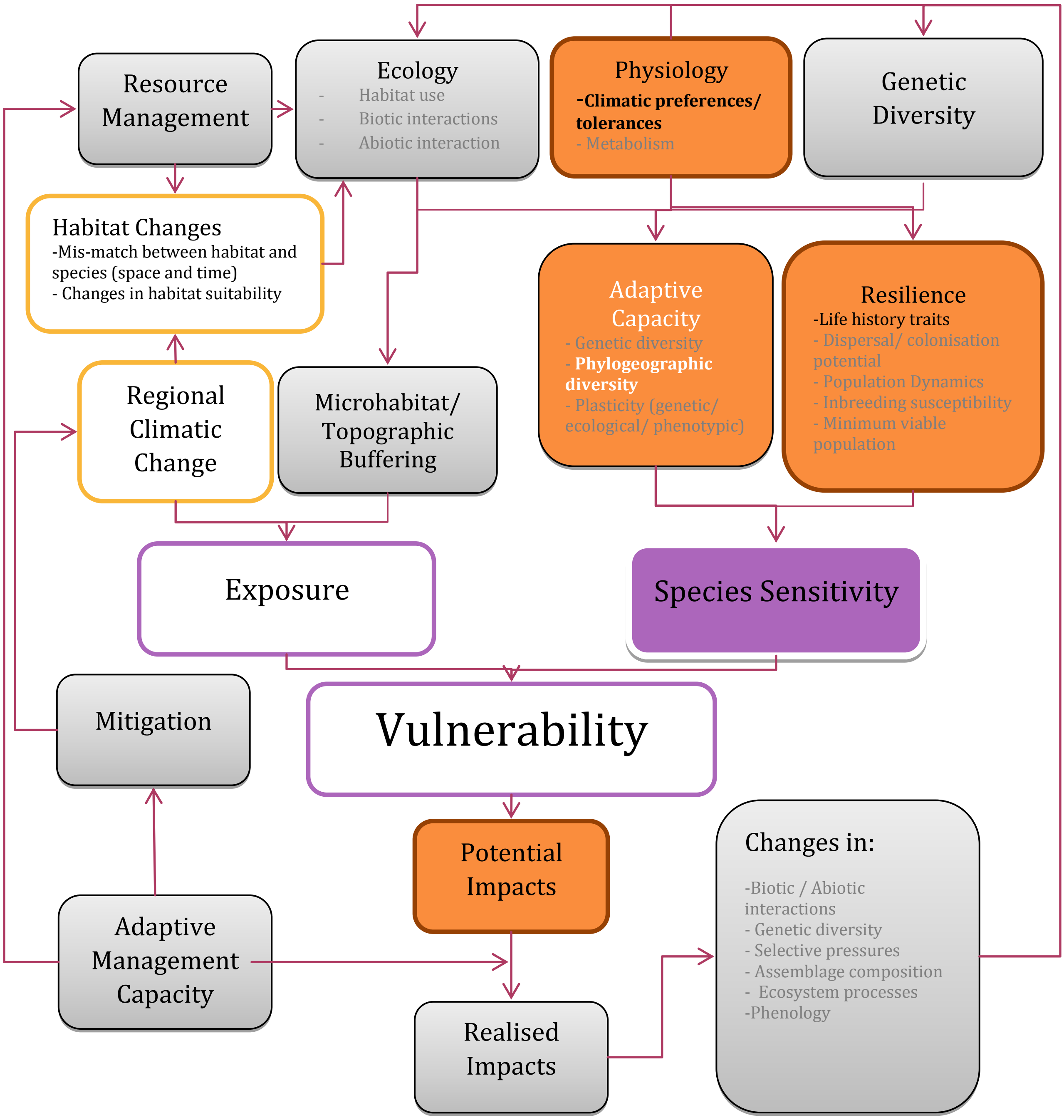


Figure 3.2 The Vulnerability Framework (After Williams *et al* 2008)

This chapter seeks to create a robust measure of sensitivity and in doing so allow the examination of species and their constituent taxa's vulnerability to climate change. The measure of Sensitivity will be determined by the species life history and ecological traits. It will then be tested against the species past exposure to climate change for robustness. It is theorised that past exposure to climate change has left a discernible fingerprint in determining species sensitivity (Turvey and Fritz 2011).

This study takes the approach outlined in the Vulnerability equation (eq.1), where vulnerability is a function of exposure and sensitivity. Exposure, in this case, is determined using Maxent (Phillips and Dudik 2008), a correlative modelling technique which assesses the extent to which climate change will alter the species distribution. This chapter examines the impact of past exposure in defining species overall vulnerabilities and giving insight into species innate sensitivities. The definition of sensitivity in this study is closely modelled on Williams *et al's* (2008) definition of Resilience accounting for species dispersal capacity and their life history traits for which there is comprehensive data. This data is used to create a single metric which describes species' individual sensitivities In an adaptation of Williams *et al*'s (2008) Vulnerability framework, (Figure 3.2), highlighted in white are the processes taken into account within this Sensitivity study.

This study concentrates on terrestrial Mammals for which there is a vast amount of data both describing a range of life history strategies and their accompanying distributions. Such large scale macrophysiological projects have been advocated for the assessment of traits across taxa (Chown and Gaston 2008).

3.1.3 What characterises Sensitivity?

Sensitivity describes the degree to which a species or individual is susceptible to stresses, for instance, more sensitive species are likely to display greater declines in fecundity or survival with small perturbations in climate (Dawson *et al.* 2011). The two factors, identified in Williams *et al* (2008) as constituents of sensitivity, namely resilience and adaptive capacity, encompass several aspects. Resilience is defined as the 'ability of species to survive and recover from a perturbation' (Williams *et al.* 2008). Adaptive capacity can be seen as the ability of a species to adapt and evolve in response to environmental challenges (Adger 2006). Resilience encompasses life history traits, dispersal and colonisation potential, population dynamics, minimum viable population and inbreeding susceptibility. Adaptive Capacity includes, genetic and phylogeographic diversity and plasticity in genetic, ecological and phenotypic characteristics (Figure 3.2). The degree to which a species is sensitive can be evaluated through observations and modelling analyses (Dawson *et al.* 2011).

A suitably robust measure of Sensitivity requires the examination of aspects of life history theory and a review of current knowledge of the basis of species sensitivities rooted in their past experiences of climate change.

Life history theory

Life history theories seek to expound upon the evolution of species traits as an adaptive response to environmental variation, they examine the interconnectedness of traits and the degree to which they are constrained by abiotic and biotic factors (Winemiller 2005). In brief, these theoretical frameworks attempt to describe the components which determine a species fitness (Nylin and Gotthard 1998). The capacity for determining species' fitness from life histories makes them invaluable for the prediction of demographic responses to perturbations in environmental conditions, such a climate change (Winemiller 2005).

The r-K selection theory: Fast versus slow life history strategies

The r-K selection theory, otherwise known as the fast-slow continuum concept, seeks to describe the relative trade-off between two life history strategies,' fast' or 'slow' (MacArthur and Wilson 1967).

Essential to the understanding of the r-K selection theory, and further visualising a species position along it, is knowledge of basic concepts of population biology, at the heart of which is the below logistic equation,

$$\frac{dN}{dt} = \frac{rN(K-N)}{K} = r_{max}\mathrm{N} - r_{max}\mathrm{N}\left(\frac{\mathrm{N}}{\mathrm{K}}\right)$$

Where *N* is the number of individuals in the population, r_{max} describes the intrinsic rate of population increase and *K* is the carrying capacity.

At one end of the continuum is the *r*-selection or opportunist's strategy, describing rapid population growth approaching rates of maximum *r* (the intrinsic growth rate), a strategy prevalent in variable and unsaturated environments, with no density or competition constraints (Calder 1984). The optimal strategy under these conditions is to maximise reproduction, putting the least required resources into each offspring and producing the largest number possible (Pianka 1970). Thus, r-selection is characterised by high productivity (Pianka 1970).

The *K*-selection strategy seeks to maintain the population in equilibrium, at carrying capacity *K*, it occurs under stable and thus saturated environmental conditions where density effects are at their maximum and competitive ability is necessary to persist (Calder 1984). To maintain a population within these conditions, replacement is the key, thus, the optimal strategy requires the maximum energy to go into the production of few, extremely fit progeny (Pianka 1970). Efficient use of environmental resources and high competitive ability characterises the *K*-strategy (Pianka 1970).

The fact that many life history traits co-vary led to the development of these alternative dominant pathways (Bielby *et al.* 2007), with several traits associated with each strategy. The *r*-selected species embody 'fast' characteristics including fast growth, reaching sexual maturity early and having large litters more than once a year with short gestation periods (Purvis et al 2000). K-selected species are characterised by 'slow' traits, reaching sexual maturity late, having slow growth rates, long gestation periods, small litters and long interbirth intervals (Purvis *et al.* 2000). However, no species is positioned at the extremes of *r* or *K* selection, but along the continuum between fast and slow life histories (Pianka 1970). The *r-K* selection theory has been utilised in many studies seeking to improve predictions of species sensitivity to environmental change (Bielby *et al.* 2007; Fritz *et al.* 2009; Isaac *et al.* 2009).

Sensitivity Traits

There is an accumulation of evidence which points to several traits that promote resilience (Isaac, 2009), and conversely traits which inflate a species extinction risk (McKinney 1997). Those predicted to bolster resilience include high reproductive rates, a fast life history and short life span, species with large geographic range sizes are also thought to be more resistant to extinction, although this rule may not apply under climate change where large spatial requirements may be disadvantageous (Williams *et al.* 2008). Species requiring large ranges to maintain a viable population will be less able to exploit small refugia (Williams *et al.* 2008).

Species ability to track their optimal climate space by dispersal and to recover quickly after a perturbation by rapid reproduction will also promote resilience (Williams *et al.* 2008). Dispersal ability will not only influence migration but also the degree to which species will employ mechanisms related to local adaptation and evolution (Lavergne *et al.* 2010). It is likely that dispersal will play different roles at the leading and trailing edges of shifting ranges in relation to persistence and adaptation (Lavergne *et al.* 2010).

Key to determining the capacity of species to recover under climate change is their ability to colonize habitats which have climatic conditions outside that of their current range, such novel climate conditions will require species to possess the ability to reproduce rapidly enough to maintain a viable population (Isaac *et al.* 2009). Thus, the degree of habitat stability selects for *r* or *K* strategists, high instability obligates that species have high reproductive capacities with fast generational turnover (*r*-selected) and high stability selects for highly competitive species with slow generational turnover (Jones 1976). Species with slow life histories, do not cope well under high mortality scenarios because they cannot compensate by increased fecundity, making them vulnerable to population extinction (Purvis *et al.* 2000). Thus, in situations where the population growth is slow, through low reproduction and immigration rates, recovery to equilibrium is slow (Jones 1976).

Species that have fast growth and mature rapidly are not impacted by disturbances as strongly as those long-lived, slow growing species; this is due to the unpredictability of disturbances under which the best strategy is always to maintain rapid growth (Lytle 2001). The dominant drivers of current extinction risk have been identified as habitat loss and climate change, thus it is expected that species with broad environmental niches are likely to be more resilient because they are better adapted to respond to changes in environmental conditions (Isaac *et al.* 2009). Isaac *et al* (2009) observed that many birds had a high capacity to recover due to their wide climatic niches, high dispersal potential and reproductive output. In mammals, Isaac *et al* (2009) found that those species which displayed low resilience were also ill equipped to recover having low fecundity, low dispersal capacity and narrow climatic niche requirements. Species belonging to higher trophic levels seem to be more vulnerable as they are reliant on those species below them in the food chain (Purvis *et al.* 2000). This combination of traits, often apparent in cases of over-exploitation, effectively reduces the capacity for populations to counteract the impact of increased mortality (Fritz *et al.* 2009). There is also evidence that small-bodied species are better able to recover from disturbances, although this is likely to be associated with the strong correlation between small body size and faster life histories (Cardillo 2003).

The risk of extinction is also intrinsically linked with population size, where fewer individuals in a population are clearly more at risk than large populations; populations which are subject to large variations in density over time are also more at risk than those which experience low temporal variability (Pimm *et al.* 1988). These population-based factors serve to accentuate the importance of maintaining viable populations, in terms of range size and abundance, in order to better able to sufficiently recover from disturbances (Purvis *et al.* 2000).

Geographical range has been linked to extinction risk and population persistence (Purvis *et al.* 2000). Large distributions may reflect large population sizes, with the effect of acting as a buffer against habit fragmentation and loss (Purvis *et al.* 2000). However, species where individuals require large discrete home ranges are more vulnerable to habitat loss and edge effects (Woodroffe and Ginsberg 1998). Large ranges may further protect against extinction by conserving high genetic variability across the population and guard against individual patches of habitat becoming climatically incompatible (Dawson *et al.* 2011). Although evidence from the paleoecological record points to the breakdown of such large blocks of suitable habitat under rapid climate change (Dawson *et al.* 2011).

In an assessment of extinction-promoting traits McKinney (1997) found that many were associated with specialisation, observing that species broadly adapted in one trait, such as diet, were often broadly adapted in others such as temperature tolerance. The degree of specialisation has also been related to local abundance and geographic range, where specialised species have low abundances and small ranges (McKinney 1997).

Phylogenetic relatedness

An accumulation of evidence suggests that phylogenetically-related species share sets of ecological traits, at least to some degree, due to their common evolutionary history (Hof *et al.* 2010). McKinney (1997)observed nesting of extinction-biasing traits in an examination of evolutionary trees constructed across different taxonomic scales, for instance they found that recent mammal and bird extinctions were clustered in particular genera and families. Research into the degree to which a phylogenetic signal is apparent among related species' ecological niches and characteristics could aid estimation of extinction-risk under future climate change (Hof *et al.* 2010). Hof *et al* (2010), in an analysis of amphibians, observed evidence of a phylogenetic signal between phylogenetically related species and their realised climatic niches. Understanding the extent to which phylogenetic-relatedness influences species niche and trait characteristics will help identification of vulnerable species for which we have little current information.

Further, strong phylogenetic signals have been successfully demonstrated across physiological tolerance traits in several groups indicating that environmental sensitivities may be conserved across species' taxonomic groups (Chown and Gaston 2008).

Plasticity of Traits

The extent to which climate change will impact species is dependent, to a degree, on the breadth of phenotypic plasticity exploitable in the face of environmental perturbations (Chown and Gaston 2008). There is little known about the types of plastic responses species can utilise in environmental situations outside those commonly encountered, extreme conditions can potentially disrupt phenotypic responses (Chevin *et al.* 2010). Phenotypic responses are expected to be physiologically–limited, particularly in the instance of body size and metabolic rate shifts (Chevin *et al.* 2010). The degree to which life history traits are plastic will depend on the fitness cost that shifting strategies will incur (Chevin *et al.* 2010). This fitness cost associated with plasticity will potentially limit a population's ability to persist in changing environments (Chevin *et al.* 2010). Research into the plasticity of traits and associated fitness costs is particularly needed among species with long generation times, such as mammals, and those with lifecycles which are dependent on seasonal timing (Chevin *et al.* 2010).

3.1.4 Why Calculate Past Exposure?

Past as the Key to the Future

The anticipated wave of extinctions is unprecedented, with predictions that rates of species losses will exceed the background rate by between two and three orders of magnitude over the next century (Balmford 1996). Multiple lines of evidence from the paleoecological record identify climate change as playing a role in species distributions, delving further into these past episodes of climate change will aide our understanding of likely future impacts (MacDonald *et al.* 2008). The clearest evidence for the influence of climate in determining biogeographic patterns exists in records of the palaeoclimatic, ecological and biogeographical history of the last 25,000 years (MacDonald *et al.* 2008; Dawson *et al.* 2011). There is little doubt that climate change during the Quaternary period greatly influenced distribution patterns of modern biota as well as their phenological and genetic evolution and giving rise to extinctions (MacDonald *et al.* 2008). Evidence for the relative Vulnerability, or extinction selectivity, of species to future climate change is thus sought in the paleoecological record (McKinney 1997).

There are few datasets of species responses to current climate change spanning a time and magnitude appropriate for assessing the likely vulnerability of species to future climate change (Willis and MacDonald 2011). Through the incorporation of an historical angle with contemporary studies of modern populations there is potential to better further understand the causal mechanisms of climate change (MacDonald 2008). Thus, exploring the impact of past exposure, the degree to which species were exposed to periods of past climatic upheaval (Williams *et al.* 2008), will help to reveal the potential impact of future climate change. Although, non-analog climates in the past will differ from those predicted into the future, they are a useful tool by which we can test the robustness of our ecological predictions (Williams and Jackson 2007). By employing a proxy of past exposure to verify our measure of species sensitivity to climate change, we can assess how robust the measure is before applying it to future scenarios. The recognition that in the past species responses to climate have been individualistic further supports the creation of Vulnerability measures based on single species (Hof *et al.* 2011).

Past Climate Change and Biodiversity Patterns

Present-day species and species groups have persisted through the transitional period 20,000 to 12,000 years ago, an era marked by high velocity climate changes, as the climate moved from glacial-interglacial phases (Dawson *et al.* 2011). However, the average velocity of warming calculated for the entire period since the Last Glacial Maximum (21,000 BP) is equivalent to 10 times slower than the rate of warming recorded in the 20th century (IPCC, 2007 p435). Table 3.1 illustrates the Quaternary period and the epochs within it to contextualize the geographic period on which this discussion focuses. Extant ecosystems are often the starting point for both predictions of past and future impacts of climate change, a principle known by palaeoecologists as 'uniformitarianism' which states that 'the present is the key to the past" (Williams and Jackson 2007). The episodes of climatic change which characterise the Quaternary are viewed as the closest analogues for understanding the impact of future climate change, (MacDonald *et al.* 2008). Over the past 2 million years there have been at least 20 such glacial-interglacial cycles, for which the best documentation of ecological and biogeographical responses are for the past 10,000-20,000 years (Dawson *et al.* 2011). The community composition of late-glacial ecosystems may appear unrecognisable, due to the individualistic nature of species' responses, however, many extant species are represented within them (Williams and Jackson 2007). It has been demonstrated from the fossil record that many taxa have survived several periods of climatic instability in the past; however, the rate of climate change was in general much slower paced giving species the opportunity to adapt whilst persisting in refugia or by shifting their distribution (Hof *et al.* 2011). Despite this predicted divergence in rates of change, and the different base mechanism, past climate change being a natural phenomenon, the paleoecological record remains highly relevant, providing evidence for the way in which species responded to differing degrees and rates of change (Willis and MacDonald 2011).

Era	Period	Epoch		Age	Ma
Cenozoic	Quaternary	Holocene			0.012
		Pleistocene	Late	‘Tarantian’	0.126
			Medium	‘Ionian’	0.781
			Early	‘Calabrian’	1.806
				‘Gelasian	2.588

Table 3.1 Geological Timeline of the Quaternary Period (Ma indicates million years ago)

Episodes of rapid climate change in the last glacial period (100±10 kyr ago) are evident in ice cores originating from Greenland (Ganopolski and Rahmstorf 2001) as well as in Mediterranean sediment cores collected in Italy (Allen *et al.* 1999). These periods of rapid change are known as Dansgaard-Oescheger (D/O) and Heinrich events. D/O climate events were centred around the Northern Atlantic and are characterised by abrupt warming of 5-10°C over a few decades or less, followed by very gradual cooling occurring over several hundred or even thousand years and a return to cold conditions (Ganopolski and Rahmstorf 2001). The timing between D/O events ranges from every 1,500 years to 4,500 years (Ganopolski and Rahmstorf 2001). Heinrich events are related to the Laurentide Ice Sheet, which covered northern America, causing surges in its extent, they occurred during the cold phases of the D/O events and effected the formation of North Atlantic Deep water (Ganopolski and Rahmstorf 2001). The Mediterranean sediment cores reveal a number of transformative fluctuations in climate occurring at more regular intervals (c. 200 years) and the changing composition of the terrestrial biosphere in response to these fluctuations (Allen *et al.* 1999).

Studies of past episodes of climate change have revealed a diverse range of responses across taxa and life history types which are likely to be repeated under current and future change (Dawson *et al.* 2011). These episodes of past climate change have been shown to have influenced aspects of genetic and morphological structure among individuals, population abundance and distributions, community composition to over-arching gradients of biodiversity (MacDonald *et al.* 2008). This response capacity is evidenced in the persistence of small populations in refugia, as well as long-distance dispersal and migration, shifts along habitat gradients, and the rapid expansion of species experiencing favourable climate conditions(Dawson *et al.* 2011). This ability to persist during challenging climatic conditions indicates that some species have natural resilience and inherent scope for adaptation(Dawson *et al.* 2011). Nonetheless, adaptive responses to past climate change remain little understood (Williams and Jackson 2007).

In looking at the effect of past cycles of climate on biodiversity, with respect to losses in genetic and species diversity across scales and by determining the situations in which species persisted against extinction, we can gain insight into species adaptive capacity and vulnerability (Dawson *et al.* 2011). Notably, there is little documented evidence from the fossil record that mass global extinctions occurred as a direct result of warming during the Quaternary (1.64Ma to present) (Willis and MacDonald 2011). However, several taxa were disproportionately affected, experiencing high levels of extinction, including large mammals (Koch and Barnosky 2006) and European tree species (Hof *et al.* 2011). Localised extinctions also occurred (Willis and MacDonald 2011), particularly among species with small range sizes (Davies and Buckley 2011).

Evidence for adaptive responses to past climate change are dominated by examples of persistence and range shifts, even during periods of rapid climate change (Willis and MacDonald 2011). The lack of documented extinctions during the period after the Last Glacial Maximum points to the fact that extant species were able to adapt by mechanisms other than range shifting and genetic evolution, for example by exploiting pre-existing phenotypic variation or retreating to stable refugia (Hof *et al.* 2011). Enquiring into the paleoecological records has more recently provided insight into the evolutionary capability of species to respond to climate change. Further, parallels with the predicted rapid rate of future climate change have been drawn with the Late Pleistocene (0.126Ma-0.012Ma) during which there is little documentation for continent-wide extinctions (Hof *et al.* 2011). Although, mechanisms responsible for past extinctions may no longer be accountable in present day species loss (Turvey and Fritz 2011). There is evidence for the extinction of several large mammals during the last deglaciation although climate change is not thought to be the driving factor (Willis and MacDonald 2011). Modern landscapes are however likely to curtail the degree to which species can adapt because of the degree to which they have been modified by humans (Hof *et al.* 2011).

Species adaptations are likely to be individualistic in form with non-analogue communities being the norm, as evidenced by past examples of novel ecosystems (Stewart *et al.* 2010; Willis and MacDonald 2011). During the last deglaciation species abundances and ranges shifted significantly, however, communities did not migrate en masse, with individual species responses varying in timing, direction and magnitude (Williams and Jackson 2007). These individualist patterns of adaptation are the result of deviations in species tolerance limits to the fluctuations of climatic variables during past periods of climate change (Davis and Shaw 2001). Similar patterns of response have been recorded for periods of earlier climate change, and there is evidence for such individualist behaviour in response to current climate change (Williams and Jackson 2007).

The Quaternary glacial-interglacial cycles exhibit a strong latitudinal gradient being of greater intensity away from the tropics (Davies and Buckley 2011). Rapport's Rule describes the phenomenon whereby species with the smallest range sizes are in the main restricted to the tropics, with the largest ranges described in high northern latitudes (Davies and Buckley 2011). As such the expectation is that tropical communities exhibit higher species richness and hold a greater number of narrow-ranged habitat specialists in comparison with higher latitude communities (Davies and Buckley 2011). This was previously thought to reflect the adaptation of species to the greater seasonal variability occurring at higher latitudes; however, it is now thought that species richness is negatively correlated with long-term glacial-interglacial cycles (Davies and Buckley 2011). Species occurring beyond the extent of the glaciated regions continued to thrive during the last ice age (Davis and Shaw 2001). Although in the Southern Hemisphere temperatures were less variable during the Quaternary, adaption was necessitated by large changes in precipitation due to changes in atmospheric conditions and ocean currents (Davies and Buckley 2011). During periods of interglacial warming species in the Southern Hemisphere and to an extent in the Northern Hemisphere expanded their ranges moving out of multiple refuges and shifting their elevations (Davis and Shaw 2001).

There are examples of extant populations which successfully persisted in situ during Quaternary climate change, for instance, in the Northern Hemisphere populations responded to the glacial retreat by expanding their range outside their full-glacial refugia northward (Davis and Shaw 2001).

Ghost of Species Past theory: Past exposure as an extinction filter

The concept that past climatic, ecological and anthropogenic perturbations have to some extent filtered out species vulnerable to future climate change, by acting as an extinction filter, is of great interest to conservationists (Balmford 1996). The central tenet of the extinction filter hypothesis is that those regions within which biotas have experienced perturbations leading to extinctions of susceptible species during past warming (transition from glacial to inter-glacial since the last glacial maximum) now appear less vulnerable to future similar perturbations (Turvey and Fritz 2011). There is evidence that indicates that those species which have undergone perturbations in their past appear more resilient, suggesting that they are pre-adapted to such threats as a result of their past (Balmford 1996). Thus, extinct species are those which failed to keep pace with the first wave of climatic change, those able to adapt and survive are consequently better adapted to persist during future perturbations (Balmford 1996).

Turvey and Fritz (2011) examined the fossil record for patterns in spatial, taxonomic and phylogenetic characteristics among the group of mammals consigned to extinction during the Holocene (past 11,500yrs); they observed that these extinctions were clustered spatially in specific taxa and geographic regions. Importantly, they further observed that these patterns showed little relation to those species at current risk (Turvey and Fritz 2011). This lack of a spatial connection between past extinctions and current extinction risk within countries lends further credence to the hypothesis, indicating that faunas in which those most susceptible species succumbed to extinction in the past now appear more resilient to future climate change (Turvey and Fritz 2011) (Figure 3.3). This phenomenon is also reflected in the fact that taxa which have experienced high proportions of extinctions in the past, such as, Xenarthans, bandicoots and bilbies, appear less vulnerable to extinction into the future (Turvey and Fritz 2011).

There is evidence that certain taxa exhibit biological traits which confer greater susceptibility to extinction (Turvey and Fritz 2011). For instance, species with low reproductive rates were most vulnerable to extinction during the Pleistocene (Koch and

Barnosky 2006). Large-bodied animals appeared to have been disproportionately vulnerable to Late Quaternary Extinction (Koch and Barnosky 2006; Turvey and Fritz 2011). In fact, Turvey and Fritz (2011), found evidence during the late Quaternary period for the successive removal of large-bodied species in extinction-prone areas, which they identified as signalling the existence of an extinction filter. The relationship between vulnerability and traits is further discussed in the section concerning the calculation of the Sensitivity measure.

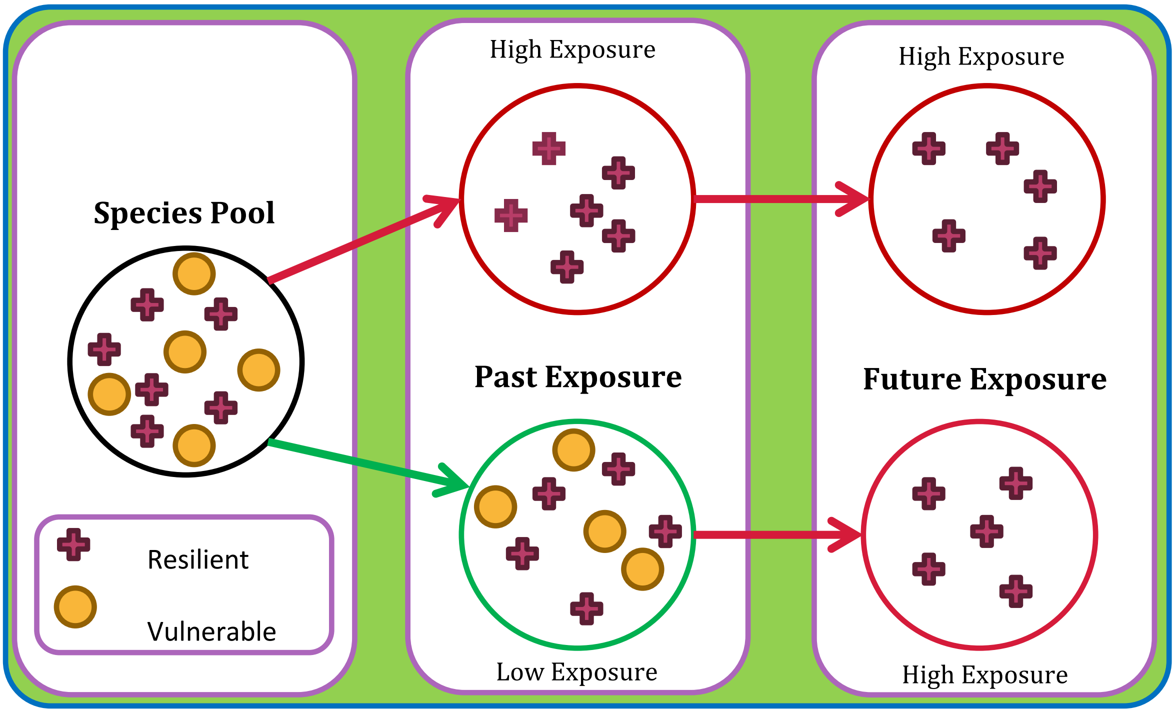


Figure 3.3 Ghost of Species Past: The Extinction Filter

The potential impact of climate change on species biodiversity is likely to operate as a function of climate change velocity (i.e. the rate of climate displacement) and its' ensuing influence on species dispersal capacity (Sandel *et al.* 2011). Investigating the impact of past climate change velocity on biodiversity can be used as an indication of the potential impact of future change (Sandel *et al.* 2011). The predicted velocity of future climate change was, until recently, believed to be unprecedented; however, recent research has shown that at the end of the last glacial period (21,000 BP) velocities approaching 4°C yr^{-1} were attained (Hof *et al.* 2011). However, the average velocity of warming calculated for the entire period since the Last Glacial Maximum (21,000 BP) is equivalent to 10 times slower than the rate of warming recorded in the 20th century (IPCC, 2007 p435). Projected velocities of future climate change suggest that species would be required to shift 300-500km per century to track their current climate niche, during past migrations species achieved on average 20-40km per century, although some species were recorded shifting 100-150km per century, these rates are far short of future velocities (Davis and Shaw 2001). Sandel *et al* (2011) in their study looking at the impact of climate change velocity on biodiversity since the LGM remarked that high velocities were associated with regions bereft of small-ranged amphibians, mammals and birds, and low endemism. Thus, regions experiencing a low-velocity of climate change acted as refugia for those small-ranged species unable to disperse effectively under high-velocity climate displacement (Sandel *et al.* 2011). This finding supports the hypothesis that modern-day susceptible species are likely to be clustered in regions where the velocity of past climatic change was marginal (i.e. where the extinction filter failed to act). Species extant in regions which have previously experienced the brunt of past cycles of climate change, particularly those in North America and Europe which were exposed to the LGM, and persisted under past abrupt climate change are predicted to be better positioned to persist under future rapid change (Hof *et al.* 2011).

Using the LGM as a proxy for past exposure

There are several advantages with regard to looking at the most recent glacial-interglacial, the Last Glacial Maximum (Willis and MacDonald 2011). The Last Glacial Maximum (LGM) marks the period ~30,000 years ago at the end of the Pleistocene when ice sheets where at their maximum extent covering much of Northern America, Europe and Asia (Clark *et al.* 2009). The transition from glacial to inter-glacial dating to ~20,000 years ago was triggered by a period of increased summer insolation in the Northern Hemisphere (Willis and MacDonald 2011). Amongst the fossil record there is evidence for species and populations which have remained in situ, adapting to the climatic shifts of the Quaternary, in the Northern Hemisphere for many taxa southern populations were stable, whereas northern populations expanded as conditions became suitable (Davis and Shaw 2001). For example, both North American and European beech trees still populate the regions of their full-glacial refuges (Davis and Shaw 2001). One advantage of studying species exposure to the climate change which characterised the Late Quaternary is that currently extant species were present during this period (MacDonald *et al.* 2008). Willis and MacDonald (2011) list five factors which add support to the relevance of analysing the glacial-interglacial transition and early to mid-Holocene in relation to future climate change impacts. These are:

1. The similar breadth of impact to current warming; the glacial-interglacial transition impacted tropical and high latitude biodiversity.
2. The period post the LGM into the early Holocene was one of significant warming for which there was no analog.
3. The degree of warming closely mirrors that expected into the 21st century, with a rise in global average temperature of 3.5 to 5.2°C, over the glacial-interglacial transition.

It may be reasoned that that extant species which have survived abrupt past climate change, have an innate ability to survive further such change due to their phenotypic variability or their ability to seek refuge in microclimatic pockets in the landscape (Hof *et al.* 2011). However, the context in which future climate change will take place is unlike that which species responded to under past climate change (Balmford 1996). Destruction and fragmentation in the landscape, absent in the Quaternary, will impede the ability of species to shift their ranges, seriously eroding species resilience (Hof *et al.* 2011). Fragmentation will not only obstruct species ability to track climate change, but also reduces the likelihood that individuals will move among populations, thus, diminishing gene flow and genetic and phenotypic variability (Davis and Shaw 2001).

3.1.5 Mammal Studies

This study will concentrate on the analysis of mammal Vulnerability because of the wealth of knowledge and accompanying data. The breadth of diversity in life history traits across mammal species means that they are particularly attractive to researchers interested in divining patterns and theories of life-history evolution (Bielby *et al.* 2007). Mammals are also the only species-rich taxon for which there is a species-level phylogeny, global maps of their distributions and in depth knowledge of biological traits (Fritz *et al.* 2009). Moreover there is clear evidence of the impact of past exposure to climate change on Mammals (Hof *et al.* 2011; Turvey and Fritz 2011). Further, the fact that a fifth of all mammal' species are currently threatened and that their populations are declining rapidly makes them a particularly appropriate group for study (Fritz *et al.* 2009).

Mammals have been recorded using a full suite of adaptation mechanisms in response to past climatic change, including shifting distributions and adaptive changes in genetic and phenotypic structure (Hof *et al.* 2011). A mass extinction of mega-faunal mammals occurred across the Americas and Eurasia during the Pleistocene-Holocene climate transition, 30 genera of large mammals became extinct in North America, and North and South America lost all mega terrestrial mammal species (>1000kg) (Gill *et al.* 2009; Willis and MacDonald 2011). During the Holocene this extinction filter purged many regions of their large species, including southern Europe, the Caribbean, Madagascar and Indonesia (Turvey and Fritz 2011). Prior to this mass extinction event in the early Pleistocene extinctions averaged 1 per 40,000 years during the Pleistocene-Holocene transition this escalated to 1 per 30 years (Willis and MacDonald 2011). Recent analysis has shown that humans may have influenced the vulnerability of large-bodied species to extinction, but that ultimately it was late Quaternary climate change which stimulated the timing, geographic area, and to some degree the magnitude of extinction (Koch and Barnosky 2006).

The analysis of fluctuations in species distributions across the Quaternary period revealed that only small range shifts occurred, with many mammal species tending to shift south or south-east during the Glacial-Holocene transition (Hof *et al.* 2011). Evidence from the period also points to the fact that some mammal species may have responded to earlier climate change in a similar way, although it is unclear whether this is a result of species possessing comparable environmental requirements or due to co-evolved biotic interactions (Hof *et al.* 2011).

3.2 Methods

The fundamental principle of this research, that a species' *Vulnerability* can be assessed on the basis of its inherent *Sensitivity* to Climate Change and the degree of *Exposure* to Climate Change it is predicted to experience, as described in the equation;

$$Vulnerability = f(Sensitivity + Exposure)$$

This section will describe the methods used in the construction and calculation of the Sensitivity measure.

3.2.1 Calculating Sensitivity

In calculating a measure of Sensitivity two well-established statistical techniques are used, principal components analysis (PCA) and simple linear regression models, justification of their use is included in the sections *Principal components analysis* and *Regression Analysis*.

Life History Traits Data and Processing

The Life-history traits (LHTd) database, from which the sensitivity measure for each species is calculated, was compiled using several sources of data. Traits available from each data source are listed in Table 3.2.

The taxonomy used is after Beck et al (2006) for the placental mammals, the Eutheria. However, because marine species were excluded from the analysis the Order Cetartiodactyla is again split into Cetacea (the Whales) and Artiodactyla (even-toed ungulates) to bring clarity to what is being modelled and investigated. The taxonomy for the Marsupials (Infraclass Marsupalia) adopts the taxonomy developed by Wilson and Reeder (2005). The full taxonomy is presented in the supplementary material S2: Taxonomy.

The LHTd is structured around the Mammal data available in the Wallace Initiative to ensure that current and future predictions of distribution are available for the Exposure calculations. The Wallace Initiative holds predictions for 1161 Mammals of which, after cleaning 1090 are used in this analysis. Cleaning involved removing records for marine mammals and correcting for errors in the taxonomy. The LHTd makes direct use of Wallace Initiative data, recording current area predictions and using the contribution of each variable to the final prediction calculated in Maxent to measure climate niche breadth.

The database PanTHERIA (Jones *et al.* 2009) contains life history and ecological trait records for 5416 mammals, these vary in terms of completeness of data. PanTHERIA holds data on 1025 of the 1143 species found in the Wallace Initiative, making it the largest contributor to the LHTd. PanTHERIA has 25 life history and ecological traits, some of which were dropped from the LHTd as unrelated to the analysis; those included in the initial analysis of variables are listed below (Table 3.2). The records were supplemented with those held in AnAge, the Animal Ageing and Longevity Database, which holds data on 1330 Mammal species (De Magalhães and Costa 2009), contributing additional records for several traits including longevity. These data were merged with those in the LHTd with PanTHERIA records taking precedence. This decision was made on the basis that PanTHERIA combines several records for each trait per species giving a more complete account of the species' traits (Jones *et al* 2009).

In addition to the life history and ecological traits, species ranked as evolutionarily distinct by the EDGE (Evolutionarily distinct and globally endangered) project (Isaac *et al.* 2007) were also flagged in the LHTd. There are 502 EDGE mammal species, which account for ~9% of the total mammal species (Isaac *et al.* 2007).

Trait	Records in LHTd	Source
Adult Mass (g)	1025	PanTHERIA; AnAge
Adult Forearm length (mm)	274	PanTHERIA
Adult Body length (mm)	553	PanTHERIA
Max Longevity (months)	486	PanTHERIA; AnAge
Basal Metabolic Rate	331	PanTHERIA
Basal Metabolic Rate/ Mass	331	PanTHERIA
Activity Cycle*	498	PanTHERIA
Sexual Maturity (days)	463	PanTHERIA
Female Sexual Maturity (days)	335	AnAge
Male Sexual Maturity (days)	245	AnAge
Gestation Length (days)	568	PanTHERIA; AnAge
Interbirth Interval (days)	291	PanTHERIA; AnAge
Age at first birth (days)	188	PanTHERIA
Litter Size	912	PanTHERIA; AnAge
Litters Per Year (n/yr)	540	PanTHERIA; AnAge
Birth weight (g)	526	PanTHERIA
Neonate Body length (mm)	16	PanTHERIA
Age at eye opening (days)	274	PanTHERIA
Weaning Age (days)	512	PanTHERIA; AnAge
Weaning Body Mass (g)	294	PanTHERIA; AnAge
Dispersal age (days)	66	PanTHERIA
Distribution size (km2)	1090	Wallace Initiative
Climate niche breadth*	1090	Wallace Initiative
Habitat Breadth*	758	PanTHERIA
Terrestriality*	755	PanTHERIA
Diet Breadth*	707	PanTHERIA
Trophic Level*	707	PanTHERIA
Home Range (km2)	337	PanTHERIA
Individual Home Range (km2)	331	PanTHERIA
Endemic*	1090	Endemics Database
Endemics Country of Origin	1090	Endemics Database
Social Group Size	220	PanTHERIA
Population Density (n/km2)	431	PanTHERIA
Population Group Size	99	PanTHERIA
Evolutionary Distinct Species	982	EDGE project
Evolutionary Distinct Species Rank	982	EDGE project
IUCN category*	1090	EDGE project
Minimum Human Population Density (n.km2)	1007	PanTHERIA
Mean Human Population Density (n.km2)	1007	PanTHERIA

Table 3.2 Life History and Ecological Traits in the LHTd (* variables are categorical otherwise continuous)

Variable Calculations

PanTHERIA

In PanTHERIA the anthropogenic variables, minimum human population density and mean human population density (persons per km^2), were calculated by Jones *et al* 2009 using the Gridded Population of the World (GPW) for 1995 (CIESIN and CIAT, 2005) across the species geographic range.

Calculating Climate Niche Breadth

Climate niche breadth was calculated using the Maxent output describing each environmental variable's percentage contribution to the final niche model. These percentage contributions were collated from each of the Wallace Initiative species models and subsequently transformed to describe the species' niche breadth. There are two environmental variables sets (Table 3.3) which the model selects from in order to make predictions; the set used is dependent on the number of species records. The four variable set is employed for species with fewer than 40 records and the eight variable set for species with above 40 records. More information on the Wallace Initiative model process is available in Appendix 2. Climate niche breadth was determined by calculating the number of variables which 'significantly' contributed to the model (i.e. >12.5% for the 8 variable set, and >25% for the 4 variable set). The number of variables contributing was then calculated as a proportion of the total number of variables available and weighted across the two groups of 4 and 8 variables. The final niche breadth is given as a percentage, higher percentages indicate broader niches.

Environmental Variables	**Code**	**8 Variables**	**4 Variables**
Annual Mean Temperature	BIO1	■	■
Temperature Seasonality	BIO4	■	■
Max Temperature of Warmest Month	BIO5	■	
Min Temperature of Coldest Month	BIO6	■	
Annual Mean Precipitation	BIO12	■	■
Precipitation Seasonality	BIO15	■	■
Precipitation of Wettest Quarter	BIO16	■	
Precipitation of Driest Quarter	BIO17	■	

Table 3.3 Environmental variable sets available to the Maxent model

Selecting Variables for Sensitivity Score

It is widely recognised that life history variables are often correlated (Bielby *et al.* 2007), thus, Pearson's correlation coefficient (r) was used to reduce the number of explanatory variables and remove variables exhibiting high collinearity. Pearson's correlation coefficient (r) measures the strength of the association between two variables (SPSS GUIDE). Correlation coefficients range from -1 to +1, the absolute value shows the strength of the association, whilst the sign represents the form of correlation, negative or positive (SPSS GUIDE). The two-tailed condition was used because there was no *a priori* hypothesis on the sign (positive or negative) of the correlations.

The Pearson's Correlation coefficient was calculated for 37 of the 42 numeric variables available in the LHTd (Table 3.2). The five variables, including the Evolutionary Distinctiveness (ED) rank, and four variables associated with the calculation of the climate niche breadth were removed prior to the analysis as irrelevant to the analysis. Figure 3.3 is a visualisation of the correlation matrix showing correlated (i.e. those variables showing associations >0.7) and uncorrelated variables (i.e. those variables with no or little association with another <0.7). The threshold value is set at 0.7> because variables which correlate to this degree are said to have a 'strong' correlation below this cut-off the correlation is assessed to be 'weak' to 'moderate' (Tabachnik and Fidell 2012).

In preparation for running a PCA, those variables presenting correlations above 0.9 were removed. For pairwise correlations, variables were removed on the basis of the number of records available, the variable with the higher number remained. For variables highly correlated with multiple others, variables were chosen on the basis of those representing the highest degree of correlation in concert with the largest number of records.

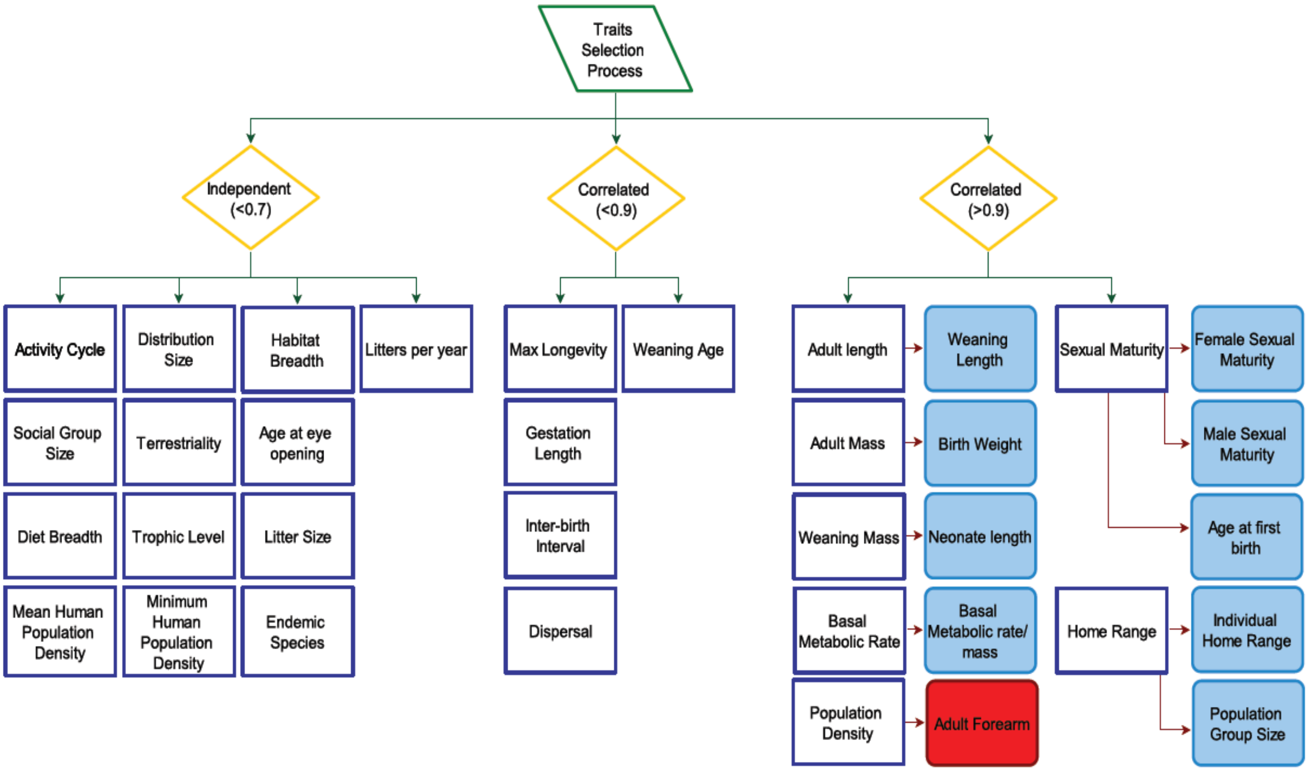


Figure 3.3 Schematic of the Trait Selection Process (blue outlined traits are included in the Sensitivity calculation, shaded blue are omitted due to multicollinearity, red removed due to low number of records.

Transformation of Variables for Analysis

Many statistical procedures, such as regression, operate with the assumption that the input variables are normally distributed and that the standard deviation of the error term of the variables remains constant across its observed range known as homoscedasticity (Osborne, 2010). If either assumption is subject to significant violation the likelihood of Type I, false positive, and Type II, false negative, errors is increased. Biological data, such as that contained within the LHTd, are often non-normally distributed (McDonald, 2009), to counter this effect variables were transformed to represent normal distributions.

The appropriate transformation of variables can improve the results of analyses even where the specific technique is deemed to be ‘robust’ to violations of either assumption (Zimmerman *et al* 2010). This is particularly important in regression analysis, which is sensitive to non-normal distributions, where transformations improve the linearity between the independent and dependent variables.

To assess for normality the continuous variables were subjected to the Kolmogorov-Smirnov test which tests for normality, a significant test indicates that the distribution is non-normal, and the variable requires transformation. Lilliefors significance correction is implemented in this case (Table 3.4) where the mean and variance of the population were unknown. SPSS also calculates the Shapiro-Wilk's W test which operates on the same premise, where a p value of >0.5 indicates a normally distributed variable (Osborne 2010).

Traits	Kolmogorov-Smirnov[a]			Shapiro-Wilk		
	Statistic	df	Sig.(*P*)	Statistic	df	Sig. (*P*)
Sexual Maturity (Days)	0.209	221	.000	.792	221	.000
Longevity (Months)	0.11	221	.000	.914	221	.000
Gestation Length (Days)	0.217	221	.000	.810	221	.000
Weaning Age (Days)	0.266	221	.000	.544	221	.000
Litters per year	0.276	221	.000	.772	221	.000
Litter Size	0.144	221	.000	.894	221	.000

a. Lilliefors Significance Correction

Table 3.4 Testing for normality in the variables

As indicated in Table 3.4 the LHTd variables required transformation since each displayed significance across both tests of non-normality. Thus, the continuous variables were log transformed, the most commonly used transformation for continuous variables of this type (Purvis *et al.* 2000; Bielby *et al.* 2007).

Data Availability and Missing Values Analysis

Before running the PCA the remaining variables were examined using a missing values analysis (MVA) in SPSS. This analysis revealed the number of records each variable and combinations of variables covered (Table 3.5 and Table 3.6). This allowed the selection of a variable set which accounted for a range of variables whilst providing the appropriate number of records to qualify for PCA and the subsequent linear regression analysis. The minimum requirement of records to maintain statistical stability for PCA is calculated by taking the proportion $n: p=>3$, where n is the number of records and p is the number of variables (Grossman *et al.*, 1991). For regression analysis the minimum number of required records is assessed using the rule of thumb $N \geq 50+ 8m$, where N is the number of records and m is the number of independent variables (Tabachnik and

Fidell 2012). The MVA listed the traits in order of the number of available records Table 3.5. The MVA also executes a pattern analysis which seeks to maximise the number of records employable in the final statistical analyses Table 3.6 .

	Records	**Missing**		**No. of Extremes**[a]	
Trait	**N**	**Count**	**Percent**	**Low**	**High**
Distribution Size (km2)	1084	0	.0	39	1
Endemic	1084	0	.0	*	*
Climate niche breadth	1084	0	.0	*	*
Adult Mass (g)	1020	64	5.9	0	50
Mean Human Population Density (n.km2)	1003	81	7.5	38	3
Litter Size	907	177	16.3	0	0
Habitat Breadth	753	331	30.5	*	*
Terrestriality	750	334	30.8	*	*
Diet Breadth	703	381	35.1	*	*
Trophic Level	703	381	35.1	*	*
Gestation Length (days)	565	519	47.9	0	0
Litters Per Year (n/yr)	537	547	50.5	2	13
Activity Cycle	512	572	52.8	*	*
Weaning Age (days)	510	574	53.0	1	16
Max Longevity (months)	484	600	55.4	0	0
Sexual Maturity (days)	461	623	57.5	0	0
Population Density (n/km2)	431	653	60.2	0	51
Home Range (km2)	337	747	68.9	0	62
Basal Metabolic Rate	330	754	69.6	0	45
Weaning Body Mass (g)	292	792	73.1	0	55
Interbirth Interval (days)	290	794	73.2	0	19
Age at eye opening (days)	272	812	74.9	0	6
Social Group Size	219	865	79.8	0	43
Dispersal Age (days)	65	1019	94	0	4

a. Number of cases outside the range (Q1 - 1.5*IQR, Q3 + 1.5*IQR).

Table 3.5 Missing Value Analysis of Life History Traits

The Missing Values pattern analysis, reported in Table 3.6 iterates across the variables recording the number of records available for a series of iterative variable sets. The final variable set of 14 traits and 213 records (highlighted in grey) was selected to maintain the widest degree of life history and ecological information whilst including the required number of records for analysis. This surpasses the minimum requirement of records for the PCA (n: p=>3), with the ratio of records across the 14 traits is 15 records to each trait. It also satisfies the minimum requirement for the regression analysis of 162 records ($N \geq 50+14*8$) (Tabachnik and Fidell 2012). These records represent 58 families and 15 orders; the full data set is presented in the supplementary material.

Trait	**No. of Species Recorded for each Variable Set**									
	22	**213**	**221**	**270**	**291**	**365**	**550**	**643**	**963**	**1084**
Distribution Size (km2)										
Endemic										
Climate niche breadth										
Adult Mass (g)					X					x
Mean Human Population Density (n.km2)	x	x				x	x	X	x	x
Litter Size				x	X				x	x
Habitat Breadth			x	x	X				x	x
Terrestriality			x	x	X				x	x
Diet Breadth			x	x	X			X	x	x
Trophic Level			x	x	X			X	x	x
Gestation Length (days)			x	x	X	x	x	X	x	x
Litters Per Year (n/yr)			x	x	X		x	X	x	x
Activity Cycle		x	x	x	X	x	x	X	x	x
Weaning Age (days)			x	x	X	x	x	X	x	x
Max Longevity (months)			x	x	X	x	x	X	x	x
Sexual Maturity (days)			x	x	X	x	x	X	x	x
Population Density (n/km2)		x	x	x	X	x	x	X	x	x
Home Range (km2)		x	x	x	X	x	x	X	x	x
Basal Metabolic Rate		x	x	x	X	x	x	X	x	x
Weaning Body Mass (g)		x	x	x	X	x	x	X	x	x
Interbirth Interval (days)		x	x	x	X	x	x	X	x	x
Age at eye opening (days)		x	x	x	X	x	x	X	x	x
Social Group Size	x	x	x	x	X	x	x	X	x	x
Dispersal Age (days)		x	x	x	X	x	x	X	x	x

Table 3.6 Pattern Analysis of Database Records ('x ' indicates that the variable is omitted)

Principal Components Analysis

PCA is employed to determine the components which best describe species life history strategies and ecologies and in combination their Sensitivity.

PCA is a well-established multivariate analysis technique. Owing to its highly versatile nature it has been used in many disciplines from engineering to psychology and in ecological problems (Torokhti and Friedland 2009). PCA has four goals, i) to determine and extract the most relevant information from the data, ii) to compress the data by summarizing patterns within the data and preserving the most relevant information, iii) to simplify the description of the data, and, iv) to analyse the structure of the observations and variables (Abdi and Williams 2010). This process provides us with an operational definition (a regression equation) of the underlying processes apparent in the observed variables. A good PCA "makes sense" in its interpretation (Tabachnik and Fidell 2012). The use of PCA is appropriate when you require a summary of the data. It provides a mathematically unique solution exactly reproducing the observed correlation matrix where all components are retained (Tabachnik and Fidell 2012). However, criticisms of PCA include the fact there is no mathematical external procedure by which the solution can be tested and that the rotation of the solution is left to expert opinion based on the interpretability of the extracted components (Tabachnik and Fidell 2012).

There are clear reasons for using PCA in the creation of a Sensitivity score. Firstly, PCA identifies the underlying processes within the data and constructs components which describe the greatest degree of variance across the dataset, identifying the variables most salient for representing life history functional groups in our measure of sensitivity. Secondly, and perhaps most importantly, is the creation of factors scores by PCA, which represent estimates of the scores individual would have obtained for each factor that was measured directly, which can be used for estimating an appropriate Sensitivity score for each species. Factor scores can also be used to predict a dependent variable using regression analysis, in this case to assess whether the factors are robust indicators of Sensitivity against a measure of Past Exposure. In reducing a large number of traits to a smaller group of components we are able to discriminate the traits important in driving species sensitivity. PCA was used to avoid falling into the preconceptions of what defines Sensitivity by determining those traits which covary statistically across the species; it identifies the major life history strategies apparent in the data. Dimension reducing techniques such as PCA and Factor analysis are commonly used to infer patterns in life history data (Bielby *et al.* 2007; Dobson and Oli 2008). Basing the Sensitivity measure on a statistical process allows both theories to be used to validate the final measure.

Prior to running the analysis the trait variables 'adult forearm length', 'adult body length', 'current distribution', 'trophic level' and 'terrestriality' were removed. The trait Adult Forearm length (mm), was highly correlated (0.9>) with several variables, including population density, adult length and adult mass, and was removed from the analysis. This removal was due to the low number of records and perceivably the degree of variance it could account for within the PCA. Further examination of the correlation matrix for the remaining variables showed strong correlation between adult body mass and adult body length, adult body length was removed as it had fewer records. 'Trophic level' and 'Terrestriality' were removed as the attributes which both described are identified as having no bearing on species sensitivity within the literature. Trophic level describes whether a species is herbivore, carnivore or omnivore. Terrestriality describes whether a species is fossorial and or ground-dwelling or arboreal.

Running the Analysis

PCA with varimax rotation was performed using SPSS on 12 traits included in the LHTd for a sample representing 213 species across 58 mammal families.

The components represent linear combinations of the observed variables and are empirical constructs driven by the variables themselves (Tabachnick and Fidell 2012)(). As a rule component loadings below 0.32 are suppressed because scores below this cut-off represent less than 10% of the overlapping variance and are therefore not robust indicators of associations across the component (Tabachnick and Fidell 2012) .

The matrix created by the PCA which shows the variables' loadings across the components can be rotated across multi-dimensional space in order to bring clarity to the PCA output components (Bielby *et al.* 2007). Varimax rotation was employed as it is the most commonly used and is particularly relevant when the factor scores are to be used in further analysis as independent or dependent variables (Tabachnick and Fidell 2012), as is the case here. Varimax is an orthogonal rotation which 'minimizes the complexity of the factors by maximising the variance of loadings on each factor' (Tabachnick and Fidell 2012). The rotated matrix explains the same degree of variance as the un-rotated matrix, although the variance is shared more equally across the factors in the rotated matrix (Bielby *et al.* 2007) .

There are several techniques to determine the correct number of components for further analysis. This reduction in components is necessitated by the fact that the inclusion of too many factors may incur the addition of noise caused by sampling fluctuations, too few and we risk masking relevant information rendering the analysis incomplete (Tabachnick and Fidell 2012). Two techniques where employed in this analysis, 1) assessment of the scree plot, and 2) The Karlis-Saporta-Spinaki Rule (Saporta 2006). The visualisation of the components in a scree plot and identification of the elbow (i.e. the 'kink' in the line) gives a good first indication of the number of components for inclusion.

The Karlis-Saporta-Spinaki rule considers the ratio of records to the number of included traits:

$$\lambda > 1 + 2\sqrt{\frac{p-1}{n-1}}$$

Where p is the number of variables and n denotes the number of records.

The traits represented in the components explaining the highest degree of variance whilst adhering to the rule are subsequently re-run with the analysis restricted to the number of salient components to maximise the variance explained across the components.

3.2.2 Testing the Validity of the Sensitivity Components

Regression Analysis

The regression analysis seeks to assess the robustness of the Sensitivity measure by assessing the degree to which the combined factor scores are able to predict the dependent variable, Past Exposure. The Past Exposure variable describes the velocity of climate change species have experienced in the past.

Regression analyses are a set of statistical techniques that allow one to assess the relationship between one dependent variable and several independent variables (IVs). In order to validate the principal components' ability to predict a species' vulnerability to future climate change, as the constituent parts of the Sensitivity measure, a regression analysis was performed with past exposure as the dependent variable. This is in line with the theory that past exposure has left a spatial imprint on modern-day species compositions by acting as extinction filter. Thus, preparation for the regression analysis entailed the creation of the dependent variable, past exposure, which is representative of past climate change.

Multiple Regression

Multiple regression is a form of regression analysis into which several independent variables are input to predict a value on a dependent variable for each entry. The form that the regression equation takes is shown in equation 1.

$$Y' = A + B_1X_1 + B_2X_2 + \cdots B_kX_k$$

Where Y' is the predicted value on the dependent variable, A is the Y intercept (the value of Y when all the X values are zero), the Xs represent the independent variables (of which there are K), and the Bs are the coefficients designated to each of the independent variables during regression. The intercept and coefficient remain constant for the prediction of the individual's values on the dependent variable, a different Y value is predicted for each entry through inserting the individual's specific X values (Tabachnick and Fidell 2012) .

Regression analysis was selected to investigate the relationship between the dependent variable, 'Past Exposure' and the independent variables which constitute the 'Sensitivity' measure. Although Regression analysis cannot imply causality of the independent variables it can infer a relationship (Tabachnick and Fidell 2012). Regression analysis is best used with a limited number of independent variables which represent the smallest, uncorrelated set of potentially explanatory variables (Tabachnick and Fidell 2012). This principle is reflected in the ten variables previously selected out by the PCA as explaining the greatest degree of variance within the LHTd. GLMs and GAMs were discounted because the variables had previously undergone normalization and these techniques specialise in regression with non-normal dependent variables (Tabachnick and Fidell 2012).

Efforts were made to improve the normality, linearity, and homoscedasticity of the residuals in the data through the removal of outliers and the transformation of variables.

Outliers are identified as those which score above the critical X^2 for α=0.05 based on the degrees of freedom which is equal to the number of independent variables. Regression analysis is sensitive to outliers that can disrupt the techniques ability to provide an accurate assessment of the relationship between independent variables and dependent variable (Tabachnick and Fidell 2012). Significant outliers were tested for by computing the Mahalanobis distance, which measures the individual records' distance (residual) from a common point. Several outliers were identified and removed form future analysis.

Regression is also sensitive to the number of input records. To calculate the lower acceptable number Tabachnik and Fidell (2012) recommend the rule of thumb, *N(number of species records)*≥50 + 8*m*, where *m* is the number of independent or predictor variables, for testing the multiple correlations. The number of full records available for input into the regression is 213 which satisfy this test.

The use of heteroscedastic data in ordinary least squares regression analysis does not significantly bias the estimate for the relationship between dependent and independent variables and the associated significance tests (Tabachnick and Fidell 2012), thus, invalidating the need for homoscedasticity testing across the LHTd variables.

The observations are also required to be independent i.e. not exhibit autocorrelation (Tabachnick and Fidell 2012). The Durbin-Watson statistic tests for autocorrelation, it reports values between 0-4 with scores indicating no significant positive or negative autocorrelation falling between 1 and 2. In this case the Durbin-Watson score is 1.76 indicating that autocorrelation is not inherent within the observations. In a further test for multicollinearity examining the tolerance statistics across the entered variables indicates its absence with scores above 0.20 and presence below this point. In this analysis multicollinearity was not apparent with none of the variables having scores below 0.20, and with all of the variables with scores exceeding 0.8.

Running the Multiple Regression

Sequential regression runs regression models across the independent variables sets, adding the sets sequentially (Tabachnick and Fidell 2012). The advantage in this case is that each components contribution in the prediction of the dependent variable can be analysed. Analysis was undertaken using the regression package in SPSS.

Past Exposure Data

Past exposure data, i.e. that which summarises the conditions experienced by species in the past is presented in terms of past velocity of climate change since the Last Glacial Maximum (LGM) (21,000 years ago). The velocity of climate change is a measurement of the local rate of change in climatic conditions across the Earth's surface (Loarie *et al.* 2009; Sandel *et al.* 2011). To calculate a localised instantaneous measure of velocity requires the division of the rate of climate change through time by the local rate of climate change across space (Loarie *et al.* 2009; Sandel *et al.* 2011).

Velocity data was kindly provided by Dr R. Davies and its calculation is analogous to that used in the paper by Sandel et al (2011), in which he was an author. The raw velocity data consist of estimates of temperature and precipitation climate change velocity at a 1.0° resolution gridded using Berhmann's equal area projection. The Behrmann equal area grid is a cylindrical map projection in which the secant cuts at 30° parallels with slight distortion in cell size towards the poles (Kennedy and Kopp 2000).

Climate Change Velocity Calculation

Climate change velocity is expressed in terms of units of distance per time, and is equal to the temporal gradient divided by the spatial gradient. Climate-change velocity holds biological relevance in that it neatly describes the local rate at which species must disperse if they are to track changing climate, whilst integrating both macroclimatic shifts with local spatial topoclimatic gradients (Sandel *et al.* 2011).

The data representing estimates of past climate used in Sandel et al's study was acquired from the Paleoclimate Modeling Intercomparison Project Phase II (PMIP2) for the two coupled ocean-atmosphere simulation models, CCSM3 and MIROC3.2 (Braconnot *et al.* 2007). These models were selected for their ability to provide a back cast of mean annual temperature estimates at the LGM at a resolution of 2.5' (Sandel *et al.* 2011). Sandel et al (2011) found that the models' estimates for mean annual temperature were highly correlated across the globe (r=0.963), thus the cell-wise mean prediction of both was used to represent LGM mean annual temperature in their estimate. Estimates of current mean annual temperature and mean annual precipitation consisted of 0.25° resolution aggregated data based on the 2.5' arc-minute WorldClim climate data (Hijmans *et al.* 2005). To calculate the temporal gradient the difference between the current mean annual temperature and the LGM mean annual temperature was computed for each 2.5' arc-minute (5km^2) cell assuming a linear range. The result of each cell was subsequently aggregated to a resolution of 0.25° by taking the mean velocity value of the aggregated cells.

The measurement of climate-change velocity is fundamentally scale-dependent and estimates change with spatial resolution, however, Sandel *et al* (2011) found that both the 2.5' and 0.25° were relatively well correlated, thus largely diminishing the impact of scale on their results. To match the resolution of past climate velocity surface with the current species distribution data calculated by the Wallace Initiative the resolution was aggregated to 1.0°. The finding that scale little impacted Sandel *et al's* (2011) velocity measurement leads me to make the assumption that scaling to 1.0° will not affect the velocity calculation and the correlation between 2.5' and 1.0° will remain constant. Thus, the estimated mean velocity of climate-change for the period LGM-present is 5.94m/yr (Sandel *et al.* 2011). This figure represents the geometric mean over the entire 21,000yr period, thus smoothing out any abrupt or short-term fluctuations in velocity during the period which may have exceeded the baseline.

Uncertainty in the paleoclimatic predictions for precipitation between the two ocean-atmosphere models at fine-scale resolution mean that Sandel et al (2011) chose to concentrate on temperature velocity since the LGM. Due to this inherent uncertainty in the precipitation data this study also focuses on temperature velocity only.

Formatting the Velocity Data

The velocity data required re-formatting to make it compatible with the Wallace Initiative data projections. The velocity data uses the Berhmann equal area projection whereas the Wallace Initiative uses the geographic co-ordinate system WGS84 consistent with that used for the BioClim (Hijmans et al., 2005) and Global Biodiversity Information Facility datasets (GBIF 2013). This was achieved using ArcGIS Desktop 10.1. (ESRI 2012) and R language packages, *SDMTools* (VanDerWal *et al.* 2012) and *raster* (Hijmans 2012). Figure 3.4 is a map of the globe showing the past climate velocities since the LGM, with red indicating high velocities scaling to dark blue for low velocities. The mapped scale is logarithmic representing a range between 0 and 168m/yr^{-1}.

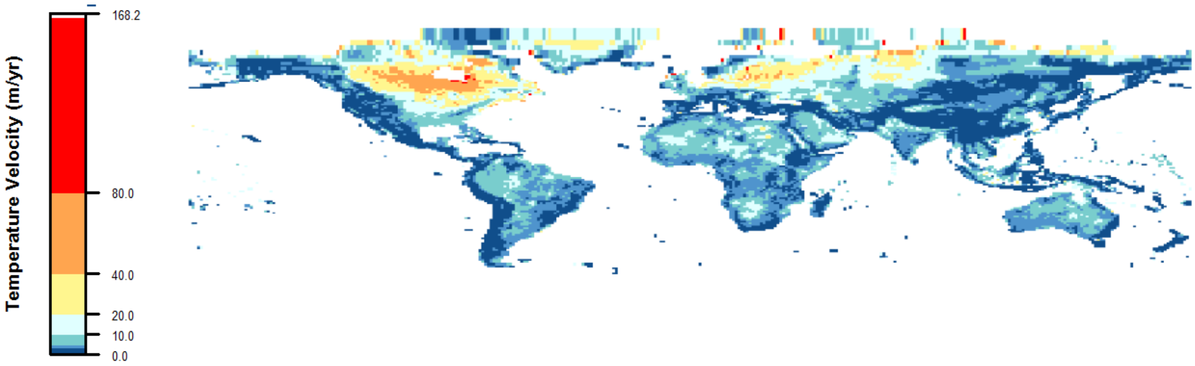


Figure 3.4 Mapped Past Velocity of ClimateChange since the Last Glacial Maximum *(after Sandel et al 2011)*

Calculating Species Average Past Exposure

Estimating a single Past Exposure value for each species required calculating the mean of the velocities experienced across the species distribution. To extract this information entailed the overlaying of the current predicted distribution from Maxent over the gridded velocity surface. The range and mean of the velocities was then calculated. This process was accomplished using SDMTools (VanDerWal *et al.* 2012) and raster (Hijmans 2012) packages in R. These mean velocity values were recorded for each of the species occurring in the LHTd and represent the operator *Past Exposure* in the *Vulnerability* equation.

In light of the fact that most species' past distributions are unknown the unclipped distributions (i.e. unrestricted) created in the Wallace Initiative were used to represent most fully the species fundamental niche. These projections represent the largest range of environmental combinations in which the species might previously have occurred. These projections are better able to capture the species past distribution and so exposure to past climate change because they encompass a wider range of possible outcomes.

Calculating the mean value using all recorded velocities experienced by an individual species would mean the measure of velocity was vulnerable to bias by the inclusion of extreme values which were not representative of the velocities experienced over the main part of the species distribution. Therefore to reduce the impact of such extremes the Outlier labelling rule (Tukey 1977; Hoaglin, Iglewicz and Tukey, 1986) was employed to remove values occurring outside the normal distribution. The rule is based on a constant 'G' by which one calculates the upper and lower bound for record inclusion based on the upper and lower quartiles of the data. First, one calculates the difference between the upper and lower quartiles; this is then multiplied by the constant 'G' which is 2.2, this number is then added to the upper quartile and subtracted from the lower quartile to give the upper and lower bounds for inclusion. The mean velocity value is then calculated across the remaining values.

The mean velocity of climate change experienced by LHTd species since the LGM was calculated as 4.71m/yr, this figure is slightly lower than the estimated global mean velocity of 5.94m/yr (Sandel *et al.* 2011). This difference may be related to the fact that velocity calculated by Sandel *et al* (2011) is not linked to specific species but calculated across the terrestrial land surface. The maximum averaged velocity of climate change experienced by any species in the period since the LGM is calculated as 128m/yr. This high past velocity was calculated for the Franklin's ground squirrel (*Spermophilus franklinii*) which occurs in the central US and into Southern Canada, the area shown Figure 3.4 to have experienced the highest velocities of past climate change.

3.2.3 Transforming Factor Scores into a Single Measure

The use of factor scores means that the measure accounts for the contribution of each of the raw variables in describing the variance among the species. The Sensitivity measure is a composite score created using the factor scores calculated by the PCAf (PCA final) across the three components. The creation of factor scores is discussed in more detail below. Thus, the equation for the calculation of Sensitivity is:

$$Sensitivity = b1C_1 + b2C_2 + b3C_3$$

Where b1,b2,b3 are regression coefficients of the components denoted by C_x. In transforming the Sensitivity measure to remove negative values the scores were rescaled by adding 10 and dividing by 10, giving the final scores as:

$$Sensitivity = \frac{(b1C_1 + b2C_2 + b3C_3) + 10}{10}$$

The creation of composite scores using PCA is common particularly in the medical sciences for diagnosis etc. and there are several methods for creating the final scores (Anglim 2009). In this case the regression factor scores, saved during the PCAf are summed together to create the final Sensitivity scores for each species.

Factors Scores

Factor scores for each component are recorded for individual species in the form of regression scores; these are useful in further analysis because they are virtually uncorrelated where the components are orthogonal (Tabachnik and Fidell 2012). Where these components are few in number, stable and easily interpretable the use of factor scores is thought to enhance further analyses (Tabachnik and Fidell 2012).

The factors scores are created by the weighting of the scores on each of the observed variables attributed to a particular factor and summing the combination of individual scores. This supposes that each individual has the same underlying component structure but different scores on the components themselves (Tabachnik and Fidell 2012). The resultant scores are linear combinations of the observed variables and take in to consideration the shared variance (i.e. what is shared between the item and the factor) and the uniqueness or error term variance (i.e. what is not measured)(Tabachnik and Fidell 2012). These scores can be regarded as a form of composite score.

Determining factor scores by regression provides estimates that are standardized , and is thus more robust than using a less complex form of computation, such as summing the scores (DiStefano 2009). The process aims to maximize the validity producing scores that are highly correlated with the factor(s) giving an unbiased estimate of the true factor scores (Distefano 2009).

3.2.4 Cluster Analysis of Traits

To determine whether the species traits identified as contributing to species Sensitivity clustered along taxonomic lines a cluster analysis was implemented. A hierarchical cluster analysis was performed in SPSS using the Ward's minimum variance method. The Ward's minimum variance criterion seeks to statistically minimise the total within-cluster variance (PSU 2013). Thus, during each step the analysis looks for the pairing which introduces the least additional variance to the total within-cluster variance after merging (PSU 2013). Each cluster begins the analysis with one point, further clusters are then determined on the basis of the weighted squared Euclidean distance between cluster centres (PSU 2013). This method was used because of the iterative way in which it proceeds using a bottom-up approach it starts at the leaves and ends at the trunk (PSU 2013). The algorithm moves up the hierarchy and stops when one over-arching cluster is achieved. It is also an approach which is appropriate for the quantitative variables represented in the Sensitivity measure (PSU 2013).

3.3 Results

3.3.1 Principal Components Analysis Results

The results of the initial principal components analysis created to determine traits defining Sensitivity using species life history and ecological traits are presented in Table 3.7and Table 3.8. These tables show the total variance explained and the rotated component matrix. This initial PCA, hereafter referred to as PCAi used the full suite of twelve variables. The PCAi extracted three factors, which exceed the required Eigenvalues >1, explaining 61.56% of the variance.

Component	Initial Eigenvalues			Extraction Sums of Squared Loadings			Rotation Sums of Squared Loadings		
	Total	**% of Variance**	**Cumulative %**	**Total**	**% of Variance**	**Cumulative %**	**Total**	**% of Variance**	**Cumulative %**
1	4.732	39.432	39.432	4.732	39.432	39.432	4.570	38.083	38.083
2	1.451	12.095	51.527	1.451	12.095	51.527	1.584	13.202	51.285
3	1.204	10.033	61.560	1.204	10.033	61.560	1.233	10.275	61.560
4	.957	7.976	69.536						
5	.821	6.845	76.381						
6	.776	6.466	82.847						
7	.652	5.434	88.281						
8	.550	4.582	92.864						
9	.303	2.523	95.386						
10	.241	2.005	97.391						
11	.193	1.608	98.999						
12	.120	1.001	100.000						

Table 3.7 PCAi Components and Total Variance

The table of communalities Table 3.8 illustrates the degree of variance accounted for across the components for each variable included in the LHTd). This assessment is important for evaluating the strength of the PCA in describing the individual components and in verifying that an appropriate number of records have been entered in to the analysis. Where variable communalities are around 0.5 or above for most of the descriptor variables the analysis is considered robust where the components are well-defined and interpretable.

Communalities

Traits	Initial	Extraction
Longevity (Months)	1	0.797
Sexual Maturity (days)	1	0.77
Gestation Length (days)	1	0.746
Weaning Age (days)	1	0.718
Litter Size	1	0.651
Mass (g)	1	0.645
Climate Niche Breadth	1	0.636
Litter per year (n/yr)	1	0.572
Habitat Breadth	1	0.563
Mean Human Population Density (n.km2)	1	0.518
Endemic	1	0.395
Diet Breadth	1	0.377

Table 3.8 PCAi Communalities across variables

The rotated component matrix Table 3.9 displays the loadings of each trait across the factors identified in PCAi. In order to achieve the model which is most parsimonious the factors were further assessed using the Karlis-Saporta-Spinaki rule which required components to achieve a minimum eigenvalue of λ=1.446 for inclusion in the final model. In this case the number of components to retain is three Table 3.7. The three components account for 61.56% of the total variance found within the data.

Rotated Component Matrix[a]

Trait	Component		
	1	2	3
Sexual Maturity (Days)	0.877		
Longevity (Months)	0.858		
Weaning Age (Days)	0.845		
Gestation (Days)	0.803		
Mass (g)	0.796		
Litters Per Yr	-0.756		
Litter Size	-0.55	0.534	
Habitat Breadth		0.704	
Human Mean Density		-0.596	
Diet Breadth		0.538	
Niche Breadth		0.538	0.79
Endemic			-0.607

Table 3.9 PCAi Rotated Component Matrix

a. Rotation converged in 7 iterations

Having identified the three components, the PCA was re-run and the number of components limited to three to maximise the variance of the variables associated with each component (PCAf). There are 213 records for 15 orders and 58 families which satisfied the full suite of traits utilised in the PCAf. Two traits, mass and mean human density were removed from the final analysis although they strongly loaded on component one (mass(g)=0.796) and component two (human mean density (n.km^2)=-0.596) respectively. Adult body mass was removed from further analysis as it known to obscure the underlying size-independent variation which in turn complicates identifying the life history traits determining species variation (Bielby 2007). Human mean density was removed because of its inherently transient nature and also because its influence would particularly distort the regressions ability to determine a correlation with past climate change exposure.

Rotated Component Matrix[a]

Traits	**Component**		
	1	**2**	**3**
Sexual Maturity (Days)	0.901		
Longevity (Months)	0.856		
Weaning Age (Days)	0.851		
Gestation (Days)	0.834		
Litters per year	-0.793		
Litter Size	-0.643	0.415	
Diet Breadth		0.783	
Habitat Breadth		0.723	
Endemic			-0.735
Climate niche Breadth			0.733

a. Rotation converged in 4 iterations

Table 3.10 PCAf Rotated Component Matrix

In PCAf the three components accounted for 66.8% of the rotated sum of squares total variance. The components describe 42.89%, 12.84% and 11.07% of the total variance respectively. The variable loadings on the three components are shown in Table 3.7. There is one complex factor, Litter size, which loads on both component 1 and 2. Explanatory descriptions for the three components are characterised as follows, 1) Reproduction and survival (Sexual maturity, Longevity, Weaning age days, Litters per year, Litter Size, Gestation Length), 2) Specialist –Generalist Continuum (Diet breadth, Habitat breadth, Litter size) and, 3) Ecology (Endemicity and Climate niche Breadth). Component 1 can be viewed as generally describing the frequency of reproductive events and the trade-off between number and quality of offspring. It describes at one end of the continuum a species which reaches sexual maturity at a young age, has a short gestation period, gives birth frequently, has large litters and weans offspring early, species at the other end, represent the opposite suite of traits. The second component is here termed the Specialist-Generalist Continuum. Where, the generalist has a wide ranging diet and can utilise a broad range of habitats. However, it is unlikely that there is a species which exemplifies this suite of traits completely, and species are likely to demonstrate a mix of these traits. Component 3, the ecology component, is indicative of the relationship between climate niche breadth and endemicity. Thus, a species which is endemic is likely to exhibit a narrower climatic tolerance.

3.3.2 Regression Analysis Results

Sequential regression was performed to determine the additive nature of each component in turn in explaining the global pattern of past exposure to climate change. The final data set contained 213 records which have entries for each of the ten traits determined by the PCAf. Past exposure is a measure of the average velocity (m/yr^{-1}) of climate change experienced across each species distribution between the Last Glacial Maximum to the current. The regression employed the logged trait variables to demonstrate each variables' contribution in the regression. Table 3.11shows the R, R^2, and adjusted R^2 across the three models, R was statistically significant from zero at the end of each step. Model 3, which has all independent variables in the regression equation, has a R^2=0.155 with 95% confidence limits from 3.897 to 5.751, F(10,213)=3.696 p=<0.01. The adjusted R^2 value of 0.113 indicates that past climate change has left a weak statistically-significant fingerprint on species assemblages, influencing the species composition by the degree of exposure to past climate change.

Thus, indicating that species sensitivity to climate change can be predicted by the trait variables selected in the PCA across the three components.

Model Summary[d]

Model	N	R	R Square	Adjusted R Square	Standard Error of the Estimate
1	213	0.365[a]	0.133	0.108	0.46361
2	213	0.368[b]	0.135	0.101	0.46534
3	213	0.393[c]	0.155	0.113**	0.46239

a. Predictors: (Constant), Weaning Age, Litter Size, Litter per year, Longevity, Gestation, Sexual Maturity

b Predictors :(Constant), Weaning Age, Litter Size, Litter per year, Longevity, Gestation, Sexual Maturity, Diet Breadth, Habitat Breadth

c Predictors:(Constant), Weaning Age, Litter Size, Litter per year, Longevity, Gestation, Sexual Maturity, Diet Breadth, Habitat Breadth, Endemic, Climate Niche Breadth

d Dependent Variable: Past Exposure

**P=<0.01

Table 3.11 Regression Model Summary

The sequential regression indicates that the addition of habitat and diet breadth adds no further power to the prediction of past exposure as they did not significantly improve R^2. Whereas, the addition of the third component variables were found to significantly add to R^2. In an examination of the standardized coefficients in Table 3.12there are five variables which are statistically significant in the prediction of past exposure; these are litter size, longevity, sexual maturity, litters per year and endemicity. However, in creating the final Sensitivity measure all 10 variables were included to maximise the degree of variance described across the full set of variables in the PCAf, and therefore make the Sensitivity as representative of the spectrum of mammal trait sets as possible.

Coefficients[a]

	Unstandardized Coefficients		Standardized Coefficients
Variables	**B**	**Std. Error**	**Beta**
Litter Size	0.217	0.08	0.295**
Gestation	0.005	0.073	0.01
Longevity	0.133	0.069	0.226*
Sexual Maturity	-0.192	0.066	-0.378**
Litters per year	-0.209	0.091	-0.244**
Weaning Age	0.035	0.061	0.059
Diet Breadth	-0.009	0.017	-0.035
Habitat Breadth	0.037	0.059	0.044
Climate Niche Breadth	0.003	0.003	0.064
Endemic	-0.277	0.149	-0.125*
Constant	4.824	0.47	

a. Dependent Variable: Past Exposure

*P=0.10 **P=0.05

Table 3.12 Regression Analysis Coefficients

3.3.3 Exploring Sensitivity

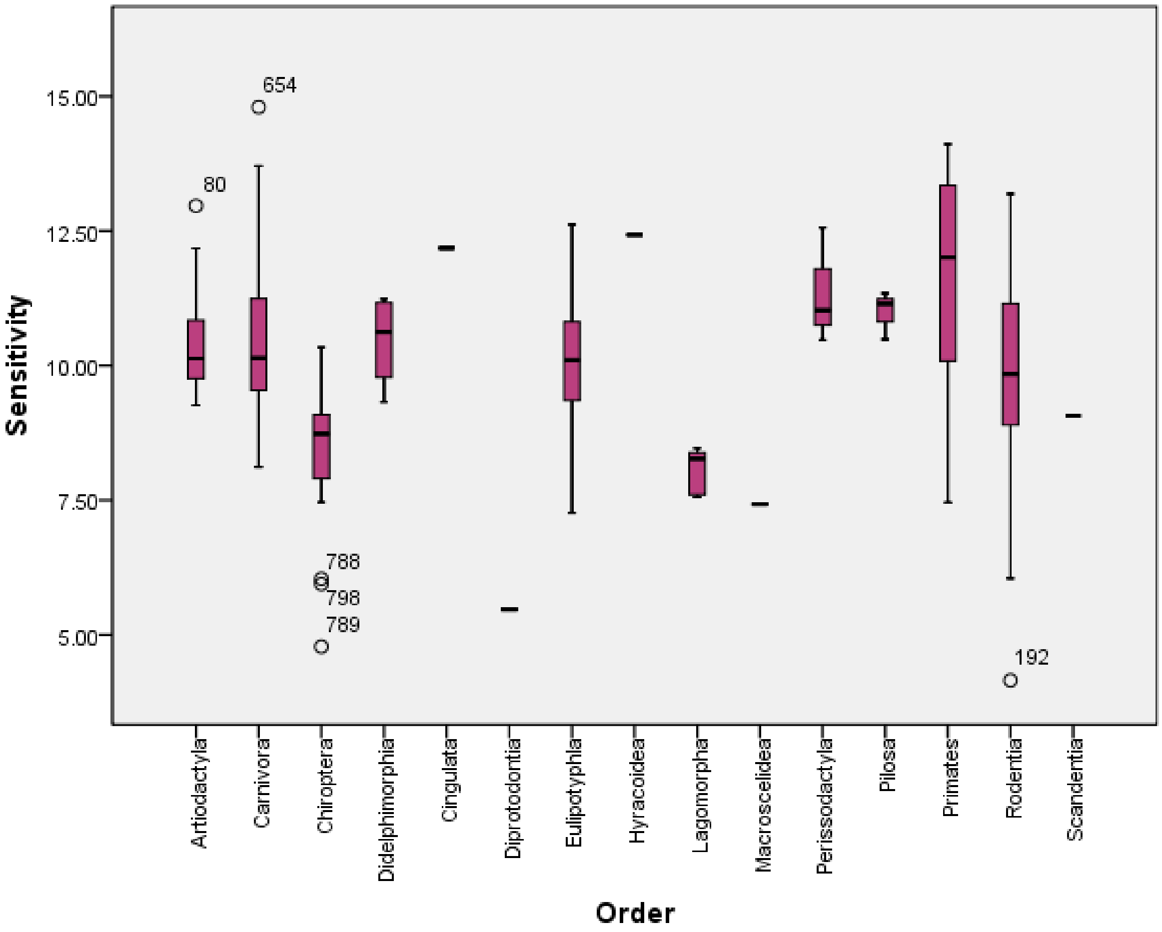


Figure 3.5 Boxplot of Sensitivity across the Orders

Sensitivity scores (*S*) range between *S=4*.15 and *S*=14.80 across the 213 species for which there is sufficient data for factor scores to be created (Figure 3.5). In a closer examination of the descriptive statistics by Order, Primates have the highest mean Sensitivity at *S*= 11.55. The Carnivora holds the most sensitive species scoring *S*=14.80 (The Walrus, *Odobenus rosmarus*), there is also a Primate species which scores very highly *S*=14.11 (The Black-capped capuchin, *Cebus apella*). Excluding those Orders for which there is less than two representative species, the Lagomorpha have the lowest mean Sensitivity at *S*=8.05 and lowest maximum score at *S*=8.46. The Rodentia have the lowest minimum Sensitivity value across the Orders (*S*=4.15) but also the largest range of Sensitivity values (S-range=9.03).

There are six outliers, species which have traits outside the characteristic range of the Order to which they belong (Figure 3.5). This range is determined by the Sensitivity values represented in the LHTd for each Order with an upper and lower bound (or quartile) being estimated to facilitate the creation of the boxplot (Figure 3.5). Three of these species belong to the same family Pteropodidae in the order Chiroptera, the Fishcheri's pygmy fruit bat (*Haplonycteris fischeri, S*=4.78), the Moluccan fruit bat (*Dobsonia moluccensis, S*=6.04) and the Greater musky fruit bat (*Ptenochirus jagori, S=5.94*). These bat species are found to be less Sensitive than the average bat species (*S-mean*=8.38). The final species in this group of least Sensitive is the Cotton mouse (*Peromyscus gossypinus S*=4.15), belonging to the Rodentia. Two species, one Artiodactyla (Red Deer *Cervus elaphus*, *S*=12.96) and one Carnivora species (Walrus, *Odobenus rosmarus, S*=14.80) are both more Sensitive than the average Artiodactyla (*S-mean*=10.38) or Carnivora (*S-mean*=10.47), respectively.

Sensitivity Descriptive Statistics

		Sensitivity Measure			
Order	**N**	**Minimum**	**Maximum**	**Mean**	**Std. Deviation**
Artiodactyla	22	9.26	12.96	10.38	0.93
Carnivora	59	8.12	14.80	10.47	1.46
Chiroptera	24	4.78	10.34	8.38	1.31
Cingulata	1	12.18	12.18	12.18	.
Didelphimorphia	5	9.32	11.23	10.43	0.85
Diprotodontia	1	5.47	5.47	5.47	.
Eulipotyphla	14	7.26	12.62	10.00	1.38
Hyracoidea	1	12.42	12.42	12.42	.
Lagomorpha	5	7.56	8.46	8.05	0.44
Macroscelidea	2	7.42	7.42	7.42	0.00
Perissodactyla	3	10.47	12.56	11.35	1.08
Pilosa	3	10.48	11.34	10.99	0.45
Primates	11	7.46	14.11	11.55	2.04
Rodentia	61	4.15	13.18	9.87	1.83
Scandentia	1	9.06	9.06	9.06	.

Table 3.13 Descriptive Statistics of Sensitivity across the LHTd213

There was a statistically significant difference between Sensitivity scores across Orders as determined by univariate GLM (F(1,14)=5.542, p=.000, η^2=0.28). The Order to which a species belonged accounted for 28% (η^2=0.28) of the variance across the Sensitivity scores indicating the order to which a species belongs has a moderate impact on individual Sensitivity score. Several orders had fewer than(N<5) records to test for significance between family differences in Sensitivity these were, Cingulata, Diprodontia, Hyracoidea, Macroscelidea, Perissodactyla, Pilosa and Scandentia.

Sensitivity across families

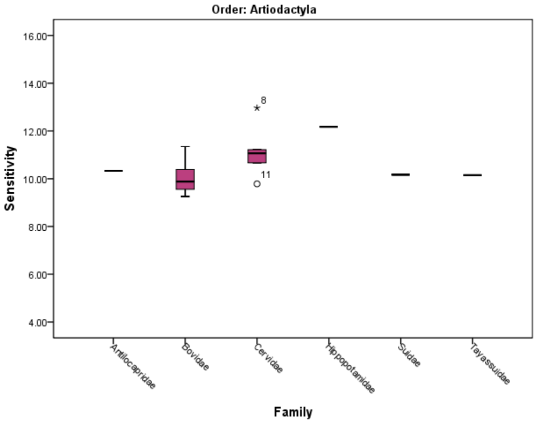
To further understand the range of Sensitivity values across Orders required looking at each Family within the set to judge whether particular families are more or less sensitive Figure 3.5. By running a GLM across all records the analysis revealed that the family to which the species belonged was statistically significant in determining the individual Sensitivity, accounting for 63% of the variance (F (1,208)=3.948, p=.000, η^2=0.63).

Order	Source	Degrees of Freedom	F	Significance *(P)*	Eta Squared (η^2)
Artiodactyla	Family Error	5 15	2.362	.090	.441
Carnivora	Family Error	11 46	5.053	.000	.547
Chiroptera	Family Error	4 19	3.093	.040	.394
Eulipotyphla	Family Error	2 11	4.323	.041	.440
Lagomorpha	Family Error	1 3	.626	.487	.173
Primates	Family Error	3 7	3.623	.073	.608
Rodentia	Family Error	17 41	1.593	.111	.398

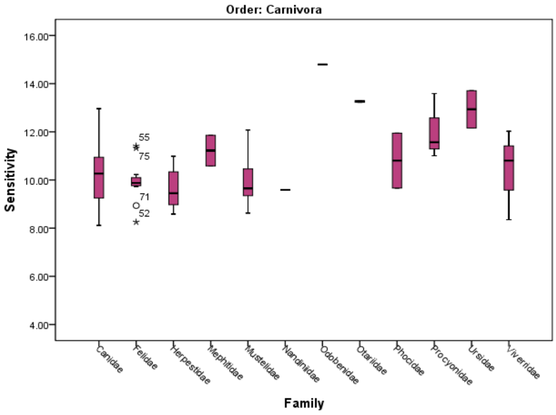
Table 3.14 Results of GLM assessing variation in Sensitivity scores by Order

There was a statistically significant difference between Sensitivity scores across Families for the Orders, Carnivora, Chiroptera and Eulipotyphla (p=0.05), as determined by univariate GLM (3.12). Two Orders 'sensitivity scores, Carnivora and Primates were strongly influenced by their constituent families (η^2=0.547 and η^2 =0.608 respectively). The remaining Orders, with the exception of the Lagomorpha, had a moderate degree of variance across the Sensitivity scores described by the families within the group Table 3.14.

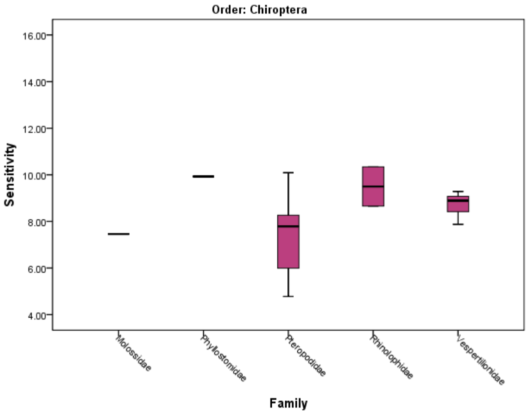
The Orders including the five most sensitive families, based on the mean (n>2) are the Carnivora which contains three families, the Otariidae (n=2,S^{mean}= 13.25), Ursidae (n=2,S^{mean}= 12.93) and Procyonidae (n=3,S^{mean}= 12.05) and the Primates which include two families, the Atelidae (n=3,S^{mean}= 12.9) and the Cebiidae (n=6,S^{mean}= 11.82). The Orders containing the five least Sensitive families are the Chiroptera, which contains two families, the Pteropodidae (n=7,S^{mean}= 7.3) and the Vespertilionidae (n=13,S^{mean}= 8.73), the Lagomorpha, containing the Leporidae (n=4,S^{mean}= 7.97), the Macroscelididea, Macroscelididae (n=2,S^{mean}= 7.42) and the Rodentia with the Hetromyidae (n=4,S^{mean}= 8.56). The Rodentia encompass the largest range between minimum and maximum Sensitivity values (*S range*=9.03). The smallest range between minimum and maximum sensitivity (*S range*= 3.7) is found in the Artiodactyla, for which there are six families represented (n=21).



a)



c)



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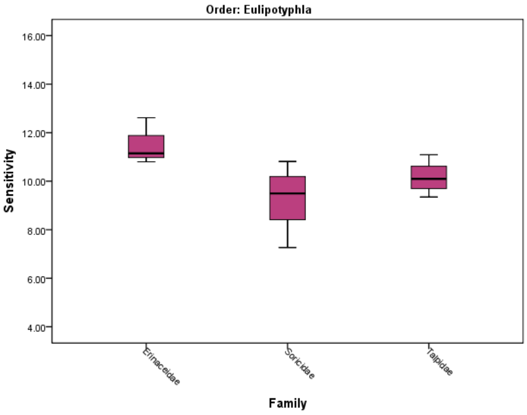

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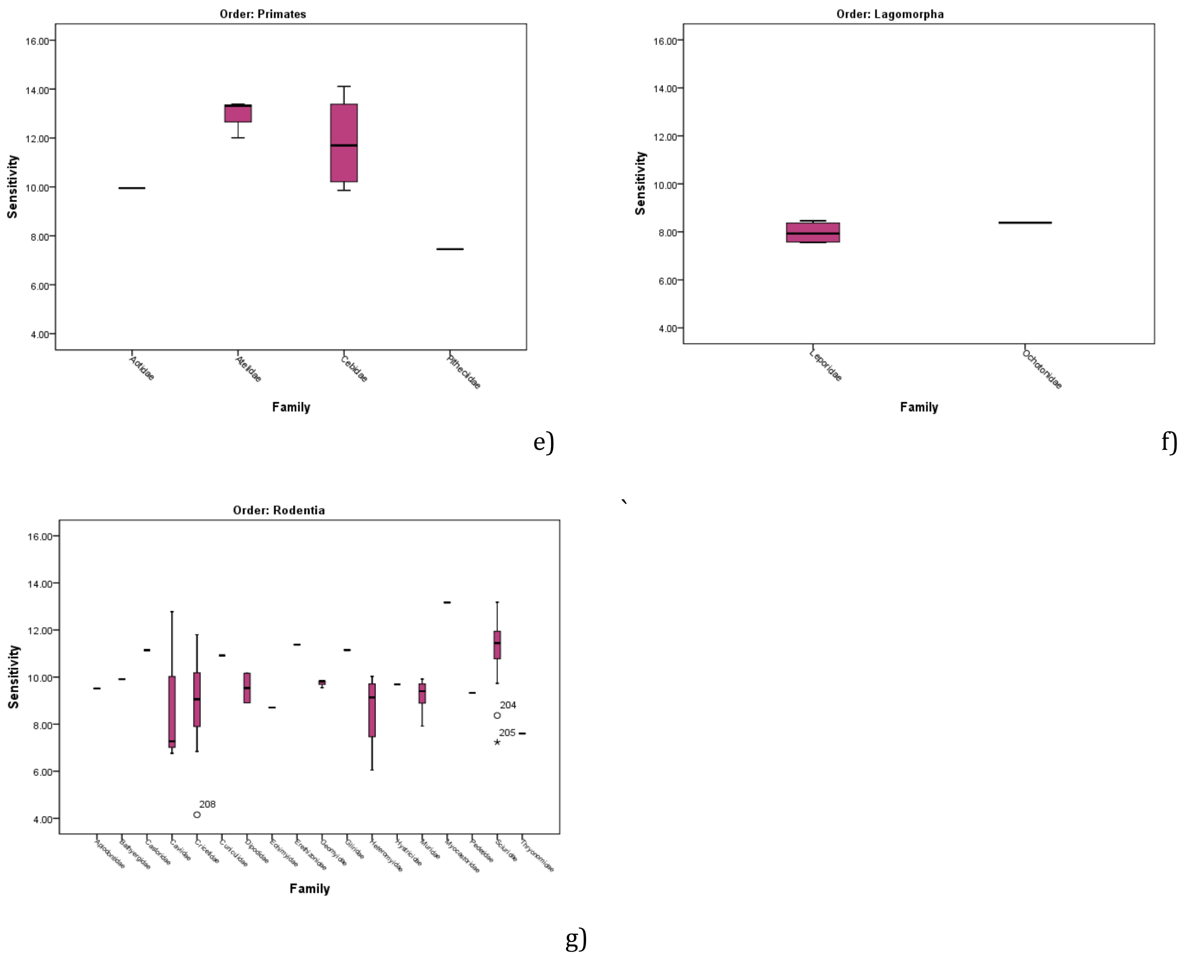


Figure 3.7 (a-g) Boxplots illustrating between family variation in Sensitivity scores across the major Orders. Outlier species are indicated by their record number.

The Artiodactyla are represented by 21 records accounting for 6 families with the largest number of records present in the Bovidae (n=12) and the Cervidae (n=5). The Bovidae have the lowest mean Sensitivity among the Artiodactyla (S^{mean}= 10.03, n=12). The Cervidae family contains the species with the largest Sensitivity score across the Artiodactyla (Red Deer *Cervus elaphus*, *S*= 12.96).

The Carnivora are represented by 58 records in the LHTd inclusive of 12 families. The Herpestidae family, the Mongooses, have the lowest mean Sensitivity (S^{mean}= *9.63,n=6*) among the Carnivora. The most Sensitive Carnivora species is a member of the Ursidae, the Bear family (Brown Bear, *Ursus arctos*, S^{max}= *13.71*). The least sensitive member of the Carnivora is a member of the Canidae family, the Bat-eared fox (*Otocyon megalotis*, S^{min}= 8.12).

The Eulipotyphla are represented in the LHTd by 14 individuals across 3 families. The Soricidae have the lowest mean Sensitivity score (S^{mean}=9.25, n=7) and also holds the individual with the lowest score among the Eulipotyphla (*S*= 7.26). The Erinaceidae are the most Sensitive family (S^{mean}=11.52, n=3) and hold the most sensitive species, the European Hedgehog, (*Erinaceus europaeus* S^{max}=12.62, n=7).

There are 11 recorded Primate species in the LHTd. The Atelidae family, which includes Spider monkeys, Woolly monkeys and Howler monkeys, are the most Sensitive among the four Primate families represented in the LHTd (S^{mean}=12.9, n=3).

There are 18 Rodentia families (n=59) represented in the LHTd. The Sciuridae family, the Squirrels, are the most sensitive (S^{eann}=11.10, n=17), also containing the most Sensitive species of Rodentia with a maximum score of *S*=13.18. The Cricetidae holds the Rodentia species with the lowest Sensitivity score (S^{min}=4.15, n=13).

Temperate and Tropical zones

To assess whether Sensitivity scores vary significantly across major ecological regions the LHTd data was split in to Tropical and Temperate species (Figure 3.6). If a species current distribution is predominantly in the tropical realm they were noted as being tropical and vice versa. This assessment was made visually using the current distribution maps available for each species on the Wallace Initiative website (Wallace Initiative 2013). Using a univariate GLM controlling for Order, Sensitivity scores were found to be not significantly different across the Tropical and Temperate zones (F (1,208)=2.717, p=.101, η^2=0.014), accounting for less than 1% of the overall variance.

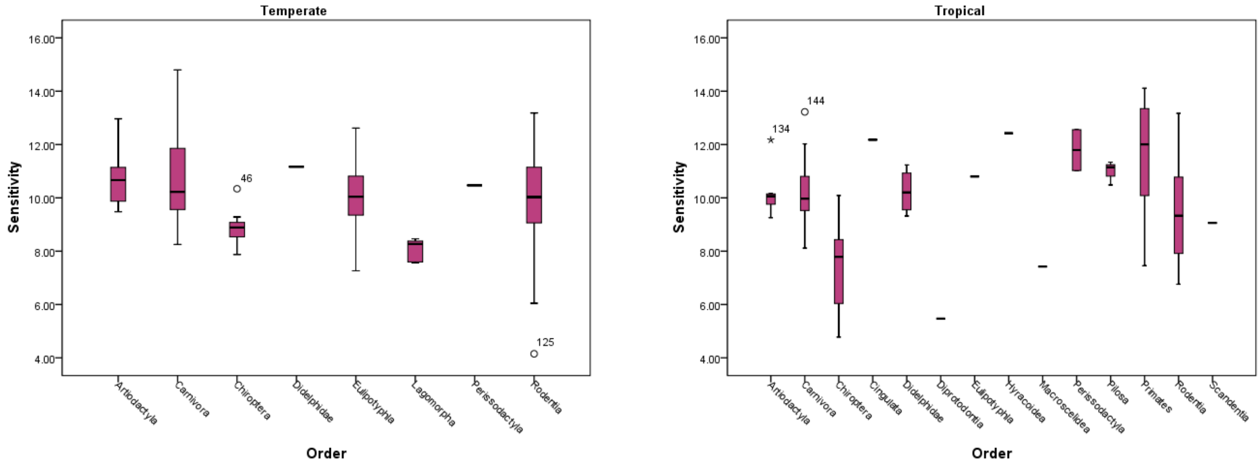


Figure 3.6 Variation in Sensitivity scores across the Biogeographic realms by Order

Sensitivity and Endemics

There are 11 Endemic species represented in the LHTd213, five rodents, four bats, a single carnivore, a primate and a possum, none of which occur in the top 10% of Sensitive species. In fact, four of these endemic species have Sensitivity values outside the range of values characteristic of their orders, being less Sensitive, these are the three Chiroptera (*Haplonycteris fischeri, Dobsonia moluccensis, Ptenochirus jagori)* species and one Rodentia species (*Peromyscus gossypinus*). A significant difference was found between Sensitivity values for Endemic and Non-Endemic species, when accounting for Order (ANCOVA, F(1,204)=65.08, p=0.00, η^2=0.24). Each of the endemic species has a Sensitivity value below the lower quartile for the Order to which they belong with the Cotton mouse (*Peromyscus gossypinus*, Sensitivity=4.15), Red-bellied titi (*Callicebus moloch* Sensitivity= 7.46), and Greater musky fruitbat (*Ptenochirus jagori,* Sensitivity=4.78) representing the lowest scores for their orders. The remaining species are the Cape Genet (*Genetta tigrina*), Common brushtail possum (*Trichosurus vulpecula),* Woodland vole (*Microtus pinetorum*), Heerman's kangaroo rat (*Dipodomys heermanni*), San Joaquin Antelope squirrel (*Ammospermophilus nelson*) and Uinta ground squirrel (*Spermophilus armatus*)

Cluster analysis of traits

A cluster analysis of the 213 species based on the traits identified in the PCAf, excluding endemicity, determined how the individual species group across the traits. Two dominant branches were identified and eight clusters, as indicated in Figure 3.9 (Branch One and Branch Two, clusters a-g). A full scale cladogram is available in the supplementary materials.

Table 3.15 illustrates the number of species represented in each of the two branches by Order. Clusters in Branch One are characterized by species with K-attributes, being long –lived, becoming sexually mature later, having few small litters with long gestation periods in comparison with those on Branch Two. It encompasses the full set of Chiroptera and Perissodactyla and the majority share of the Carnivora, Artiodactyla and Primates. The Pilosa, Hyracoidea, Diprotodontia and Cingulata are also fully represented. Clusters on Branch Two are characterised by *r*-selected traits with multiple litters of multiple offspring per year, reaching sexual maturity young and having short life spans. Branch Two represents all the Eulipotyphla, Scandentia, Macroscelidea and Didelmorphia and the majority of the Rodentia and Lagomorpha. It also includes 21 of the 58 Carnivora species comprising of small bodied carnivores such as weasels and ferrets, mongooses, genets and raccoons.

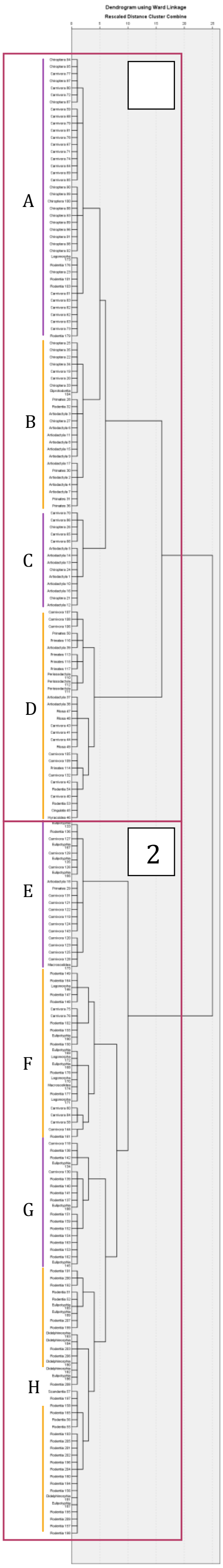


Figure 3.9 Cladogram determined by Sensitivity Traits (excluding Endemicity)

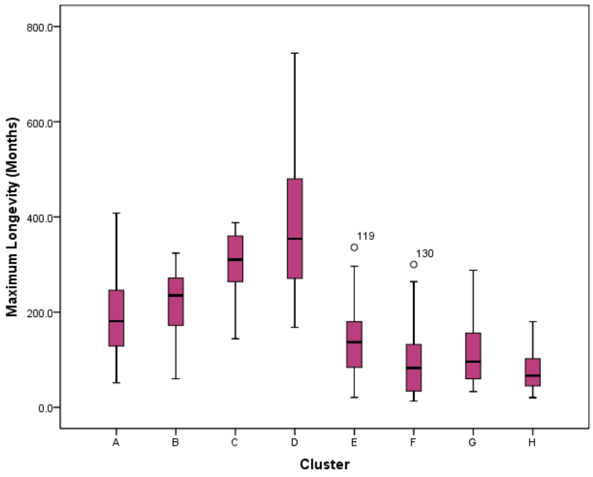
Interestingly, although in the main the major orders cluster on the branch expected, i.e. dominant *K* or *r*-selected, with the exception of the Carnivora which is split across the two branches, species do not necessarily group together by cluster below this level of organisation at the level of family or genus (Table 3.15).

Family	**Branch One (n)**	**Branch Two (n)**	**Cluster(s)***
Artiodactyla	20	1	**B**,C,D (E)
Carnivora	37	21	**A**,(B),C,D,**E,**F,(G)
Chiroptera	24	0	**A**,B,C
Cingulata	1	0	**D**
Didelmorphia	0	5	**H**
Diprotodontia	1	0	**B**
Eulipotyphla	0	14	E,F,G,H
Hyracoidae	1	0	**D**
Lagomorpha	1	4	(A)**F**
Macroscelidea	0	2	E,F
Perissodactyla	3	0	**D**
Pilosa	3	0	**D**
Primates	10	1	**B,D**, (E)
Rodentia	7	59	(A), (B),(D), (E),F,**G,H**
Scandentia	0	1	**H**

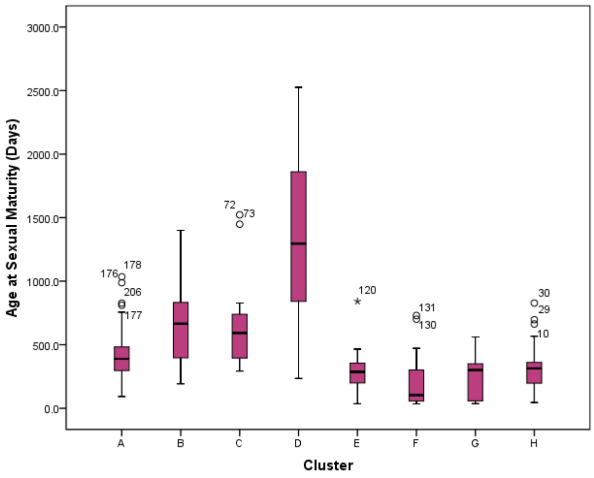
* Dominant clusters in bold, bracketed for outliers

Table 3.15 Clusters defined by number of species from each Order

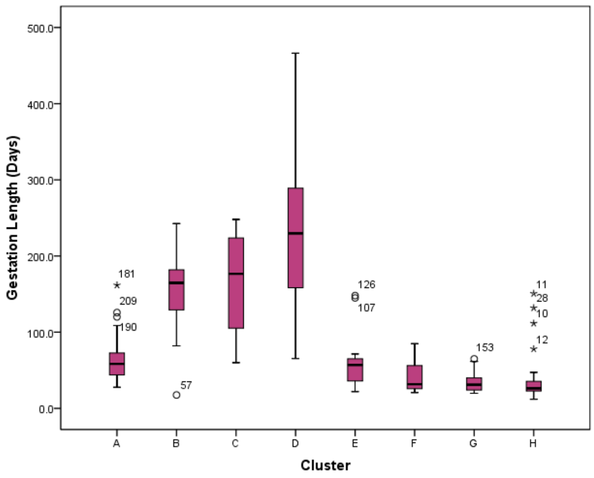
In a closer look at within-cluster variation in traits it is clearer how the traits interact with one another (Figure 3.10). The clusters confirm the theory expounded by Bielby *et al* (2011), that species are neither wholly K-selected nor wholly *r*-selected but appear along a continuum. Cluster D (Branch One), which includes all the Perissodactyla (n=3) and Pilosa (n=3), the majority of the Primates (n=6) and 11 Carnivora, has the greatest affinity to the archetypal K-selected species. Cluster A (Branch One) in which the Chiroptera are the dominant order is characterised by species reaching sexual maturity early relative to the other clusters in Branch One, with short gestation periods and multiple offspring in a litter with a short duration to weaning but also narrow diet preferences and maximum longevity exceeding those of branch two. As such these species are atypical K-strategists in that they possess multiple attributes, by which they could be classified as *r*-selected, but their relative longevity, narrow diet and number of litters per year places them on Branch One. The traits most associated with *r*-selected species, such as short lifespan, early sexual maturity, short gestation length with multiple offspring and several litters a year, and wide diet are embodied by cluster H (Branch Two) which is dominated by Rodentia families (n=28 of 38 species). Cluster F, also on Branch Two, and which encompasses the four Leporidae species (rabbits and hares), two Eulipotyphla families and the Macroscelidea (Elephant shrews) amongst others, are another interesting group in that they conform to the majority of *r*-selected traits, being the grouping with the most litters per year (up to 7 with a mean of 3.8), but having a much narrower diet than the other clusters on Branch Two.



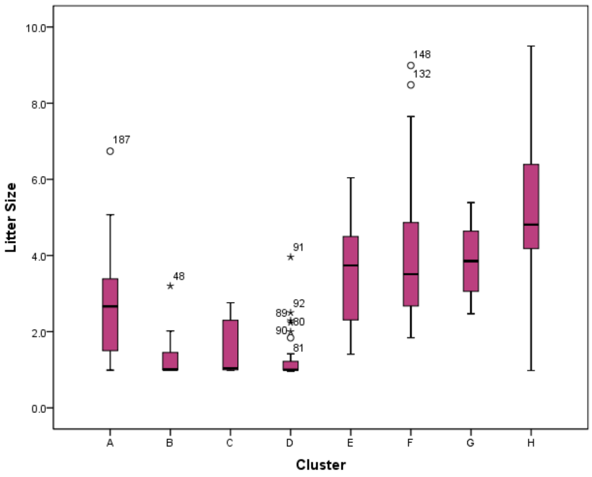
a) Maximum Longevity (Months)



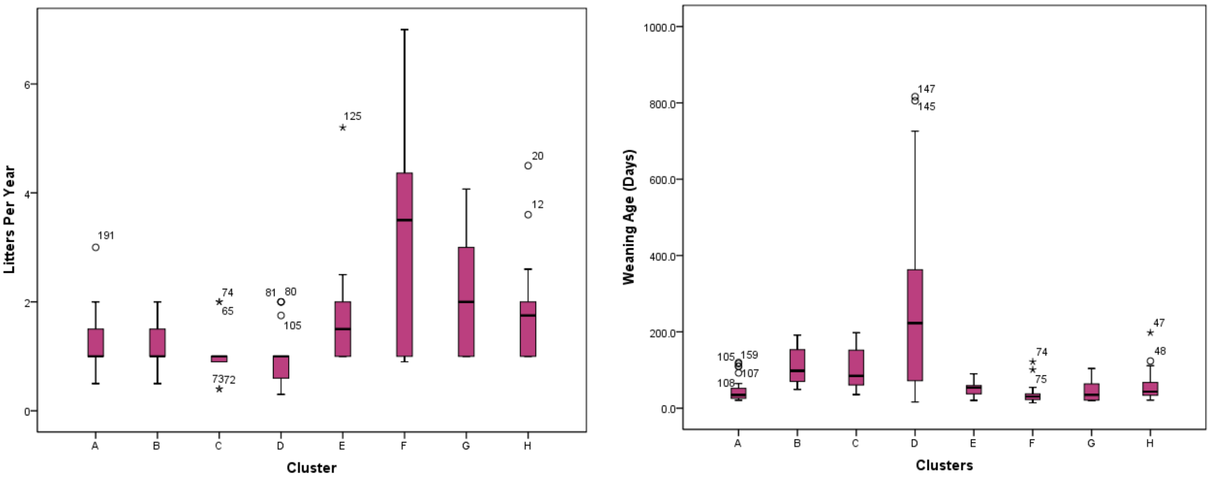
b) Age at Sexual Maturity (Days)



c) Gestation Length (Days)

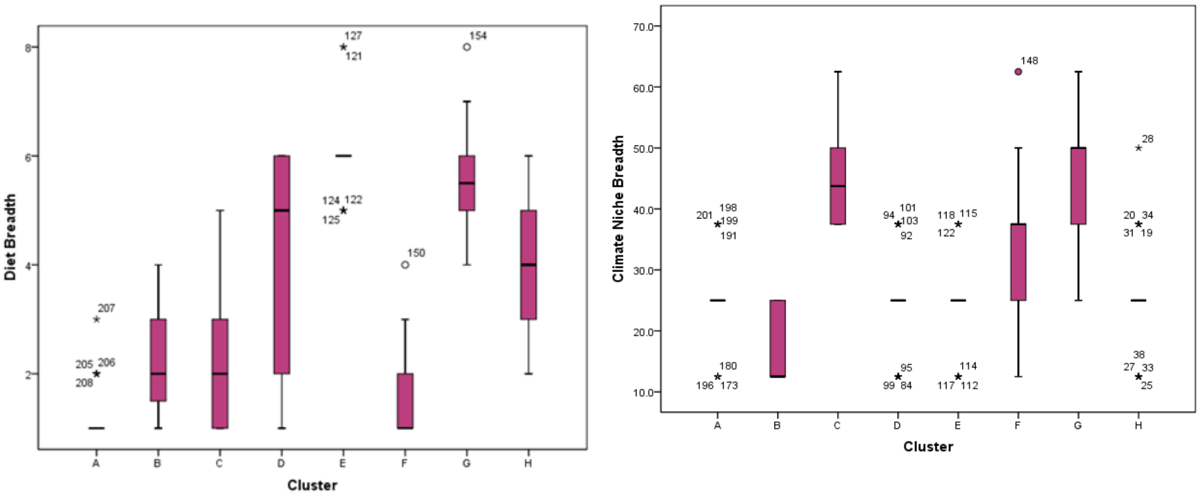


d) Litter Size (N)



e) Litters per year

f) Weaning Age (Days)



g) Diet Breadth

h) Climate niche breadth

Figure 3.10(a-h) Boxplots showing the variation in traits across the clusters

In a cluster analysis of Sensitivity, five major clusters were created which describe the groupings across the Sensitivity scores. However, Sensitivity scores do not cluster along the lines of the *r*-K continuum in a similar pattern to the traits because moving away from the raw data to a composite score removes the nuances in the individual species traits structures (Figure 3.11). Thus, species may score the same overall Sensitivity but be sensitive on different traits.

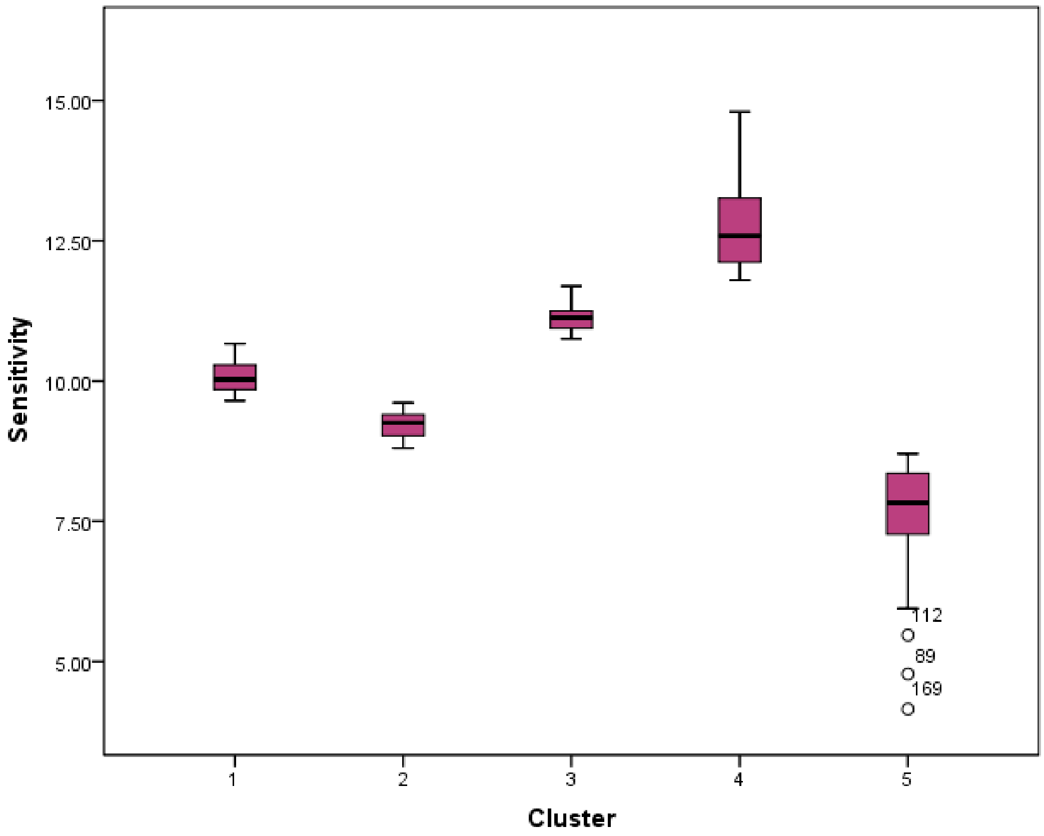


Figure 3.11 Range of Sensitivity Scores across Clusters

3.4 Discussion

This research sought to identify those species most Sensitive to climate change, but more importantly the Orders and their composite traits associated with Sensitivity. It explores the degree to which species life history and ecological characteristics can be used to determine an individual species' Sensitivity to disturbances in the landscape, in this instance to climate change.

3.4.1 What are the specific life history and ecological traits which in combination determine a species Sensitivity?

The result of the PCAf, created to elucidate patterns in traits across the species in the LHTd, determined three components, 1) Reproduction and survival (Sexual maturity, Longevity, Weaning age days, Litters per year, Litter Size, Gestation Length), 2) Specialist –Generalist Continuum (Diet breadth, Habitat breadth, Litter size) and, 3) Ecology (Endemicity and Climate niche Breadth).

The variables contributing to component 1 'Reproduction and survival' are judged to correlate with the expectations of the r-K selection theory (Pianka 1970), describing through the correlations across the component, the frequency of reproductive events and the trade-off between number and quality of offspring. The nature in which the variables correlate describes the fast life history and short life span viewed as prerequisite to high species resilience. This finding confirms that of Dobson and Oli (2007) who used PCA to determine whether Mammal life history traits lined up along the fast-slow continuum, their first component showed co-variation of survival and longevity traits said to reflect the expected trade-off of reproduction and survival.

The second component the 'Specialist-Generalist Continuum' describes environmental resource use correlated with reproductive capacity. It thus also corresponds with the expectation in r-K theory that competition for resources is connected with fewer fitter offspring (Pianka 1970). Further, it concurs with resilience theory, in which broad diet and habitat specialisation enhances species resilience (Issac *et* al 2009). The third component, which describes the species 'Ecology', is outside the framework of r-K theory; however, it does fall within the principles of resilience theory. The negative correlation described in the Ecology component between endemicity and climate niche breadth is allied with the principle that a large geographic range and broad environmental tolerance promotes resilience.

3.4.2 How does this combination of life history and ecological traits determine the level to which Orders are Sensitive?

The Sensitivity measure needed to reflect the constituent components identified in the PCA. It also needed to be directly relatable to the degree to which a species is defined as being tolerant to environmental disturbances, including climate change, in the literature.

Which traits confer Sensitivity to Climate Change?

A key factor in determining the capacity of species to recover under climate change is their ability to colonize habitats which represent changed climatic conditions, such circumstances will require species to possess the ability to reproduce rapidly enough to maintain a viable population (Isaac *et al.* 2009). This factor along with dispersal and adaptive capacity will play a vital role in determining species survival.

Thus, the degree of habitat stability selects for *r* or *K* strategists, high instability obligates that species have high reproductive capacities with fast generational turnover (*r*-selected) (Jones 1976), putting the least required resources into each offspring and producing the largest number possible (Pianka 1970). High stability selects for highly competitive species with slow generational turnover (*K*-selected) (Jones 1976). To maintain a population within these conditions, replacement is the key, thus, the optimal strategy requires the maximum energy to go into the productions of few, extremely fit progeny (Pianka 1970).

Species that have fast growth and mature rapidly, are generalists and have broad environmental niches and high dispersal capacity are not impacted by disturbances as strongly as those long-lived, slow growing species (Williams 2008). This is due to the unpredictability of disturbances under which the best strategy is always to maintain rapid growth (Lytle 2001). Species with slow life histories, or which are isolated, do not cope well under high mortality scenarios because they cannot compensate by increased fecundity, making them vulnerable to population extinction (Purvis *et al.* 2000). Species which have a narrow diet breadth are also thought to be more sensitive than omnivores because they are unable to exploit a wide range of different food types (McKinney 1997).

The Sensitivity measure needed to effectively describe the relationships between life history and ecological traits described in the PCAf with those described in the literature as conferring resilience or inducing susceptibility. Thus, traits which are recognised by theory as bolstering a species' tolerance to disturbances are represented as a low Sensitivity score and vice versa.

In regards to abundance data being absent in the Sensitivity measure, large distributions are theorized to reflect large population sizes (Purvis *et al.* 2000), thus the measure of distribution size can be said to serve as a proxy when utilized in the future calculation of Vulnerability. It is noted however, that this relationship is flawed for those species requiring large discrete home ranges (Woodroffe and Ginsberg 1998), and so conclusions on the effect of abundance on determining Sensitivity are not included here.

Do the basic relationships across the Orders relate to the theory surrounding Sensitivity?

This section examines whether the Sensitivity measure successfully reflects the relationship between r-K and resilience theory in determining which species are most and least Sensitive to climate change. To determine whether the measure of Sensitivity reflects directly the traits identified as conferring sensitivity a comparison between the Orders across the constituent traits is shown in Figure 3.12. The mean values of each trait represented in the PCAf components were calculated for each of the major Orders (those with more than 5 species represented in the LHTd213). These values are then placed according to the principles of the *r-K* continuum, for instance an Order with a short gestation period would be placed towards the *r-selected* extreme and vice-versa. There is no Order placed at the extremes of the continuous variables because the upper and lower extents of each are unknown since not all Mammal Orders are represented in this analysis of Sensitivity. However, for three categorical traits Orders are positioned according to the known extents of the PanTHERIA database (Diet (1-8) and Habitat breadth (1-4)) and climate niche is represented as a percentage.

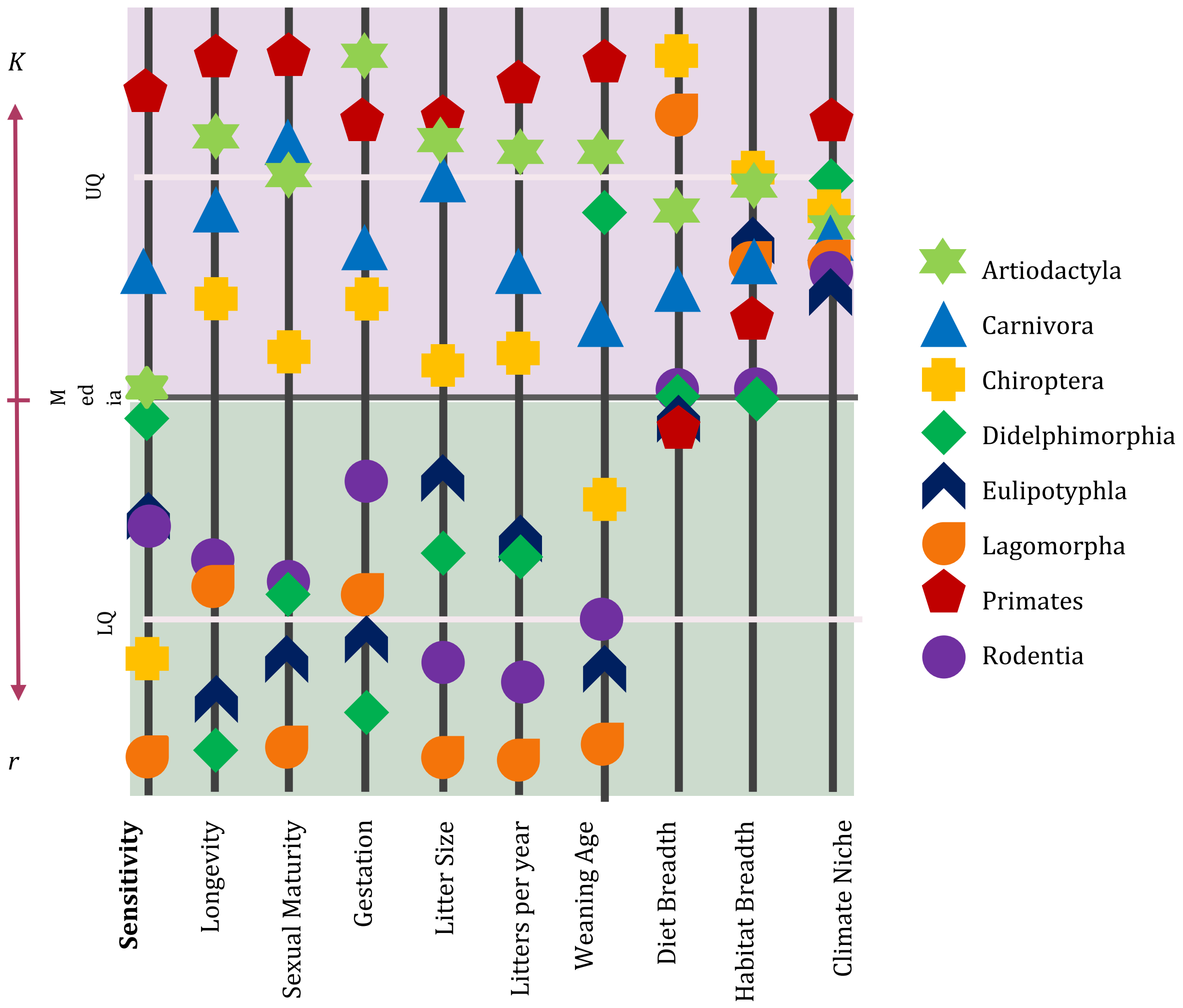


Figure 3.12 Order mean values by trait positioned according to the principles of the r-K continuum

There is no one Order which exemplifies the extremes of *r*-selected or *K*-selected traits, having traits which each occur within the upper (UQ) or lower (LQ) quartiles of values. As previously discussed, species rarely display entirely *r*-selected or entirely *K*-selected traits being positioned at a point between both extremes (Pianka 1970). The *K*-selected Orders, those for which the bulk of traits fall within the *K-selected* region of Figure 3.12, are Artiodactyla, Carnivora, Chiroptera and the Primates. The *r*-selected Orders include the Lagomorpha, Eulipotyphla and Rodentia. The Didelmorphia are positioned mid-way between the two extremes, with five traits located in the *r*-region, one trait firmly in the *K*-region and two at the mid-way point.

Within the major Orders (those with 5 species records and above), the Primates are identified as on average the most Sensitive (Sensitivity=11.55) and the Lagomorpha the least Sensitive (Sensitivity=8.05). The Primates mean values for eight of the nine PCAf traits are located toward the K-selected extreme, with seven occurring in the upper quartile of values. This prominence of *K*-selected traits would validate their position as most Sensitive amongst the Mammal Orders represented in the LHTd. The trait which is placed towards the *r*-selected extreme is diet breadth, primates are omnivorous exploiting many different food types within their diet, and this capacity may serve to reduce their overall Sensitivity. The Lagomorpha, are placed at the opposite end of the Sensitivity scale, with six of the nine traits being placed towards the *r-selected* extreme. Four of these traits fall within the upper quartile of values, indicating a short period to sexual maturity, large litter sizes, multiple litters a year and a short period to weaning age. Each of these characteristics place the Lagomorpha firmly within the *r-selected*, 'fast', end of the continuum which justifies the Order's low Sensitivity value. The three traits which occur toward the *K*-selected extreme are diet breadth, habitat breadth and climate niche. The lagomorphs are obligate herbivores, ground-dwelling species predominantly associated with grassland, shrubland and forest (IUCN Red List 2013) which might explain why as a group they score towards the *K*-selected end of the spectrum.

Do the Orders cluster along the r-K continuum?

In comparing Sensitivity scores with the pattern of mean values illustrated across the trait variables each of the Orders positions along the continuum can be viewed as aligning with the final Sensitivity score, apart from the Chiroptera. As hypothesized those Orders which display predominantly *r*-selected traits have low Sensitivity scores and vice-versa. It would appear that the Chiroptera should be additionally Sensitive, however, although 8 of the nine traits are placed in the *K*-region the Sensitivity=8.38, placing the Order just above the Lagomorpha. A limitation associated with the Figure 3.12 is that the values represented are mean scores and do not show the range of the data within the individual Orders. This explains why the Chiroptera appear to have *K*-selected traits but score a low mean Sensitivity=8.38. Within the Chiroptera are two of the five least Sensitive families represented in the LHT213, the Pteropodidae (Sensitivity=7.3) and Vespertilionidae (Sensitivity=8.73) however, the Order also holds a number of species among the Most Sensitive (n=8).

It is important to recognise that in the definition of the Sensitivity measure each trait is weighted by the degree to which it describes variance across the LHTd, creating a unique score for each species, the regression factor. These regression factors are subsequently summed to create the Sensitivity score. Thus, it is unlikely that the individual trait scores will align perfectly with the Sensitivity scores as an effect of the variables weighting.

Do the Orders cluster by traits?

Tolerance limits are thought to be phylogenetically constrained meaning that a representative species may be appropriate to describe the taxa (Hoegh-Guldberg *et al.* 2008). To investigate whether this hypothesis can be verified in relation to the Mammals and their Sensitivity a cluster analysis using the traits contributing to the Sensitivity measure was performed. This identified two major branches along one sit the major part of the Artiodactyla, Chiroptera and Primates species (primarily *K-selected Orders*) and along the other sit the Didelmorphia, Eulipotyphla, Lagomorpha and Rodentia (primarily *r*-selected Orders). Thus, the Orders can be said to group by the major features of the *r*-K continuum at this initial juncture. The only Order to break this rule is the Carnivora. The Carnivora are split across the two branches, with 63% of species on the *K-selected* branch and 37% of species on the *r*-selected branch. The Carnivora family groups are not consistently clustered across the two branches, with the Felidae (cats) being the only family to cluster entirely on the *K-branch*.

For the majority of Orders represented in the LHTd213 it is possible to determine the extent to which a species may be *r-K selected* based on the position along the continuum the Order to which they belong is located (GLM, F=(14,207)=5.58, p=0.00, η^2=0.28). This is in broad agreement with Dobson and Madan (2007) who in a study of life history traits found that the historical pattern of ancestry at the Order and Family level strongly influenced individual species life history traits with phylogeny explaining 66-85% of the variation in life history traits. Species cluster by family within one of the two branches in most cases, although this clustering is not maintained at the node level (A-G) for many families. This complicates the degree to which one can infer the species subsequent Sensitivity based on the family to which it belongs. Therefore, although one is able to infer with some accuracy whether a species is *r-K* selected and likely to be resilient based on other species in their family, it is less straightforward to say by how much they are Sensitive based on species within the same family.

3.4.3 Did past exposure to climate change play a role in determining patterns of species Sensitivity in the landscape?

What relevance does past exposure have to predicting Sensitivity?

Present-day species and species groups have persisted through the transitional period 20,000 to 12,000 years ago, an era marked by high velocity climate changes, as the climate moved from glacial-interglacial (Dawson *et al.* 2011). Studies of past episodes of climate change have revealed a diverse range of responses across taxa and life history types which are likely to be repeated under current and future change (Dawson *et al.* 2011). This response capacity is evidenced in the persistence of small populations in refugia, as well as long-distance dispersal and migration, shifts along habitat gradients, and the rapid expansion of species experiencing favourable climate conditions (Dawson *et al.* 2011). Investigating the impact of past climate change velocity on biodiversity can be used as an indication of the potential impact of future change (Sandel *et al.* 2011) and can provide insight into species adaptive capacity and vulnerability (Dawson et al 2011).

To examine whether the species Sensitivity measure is robust, a regression analysis was performed using a measure of exposure to past climate as the dependent variables and the Sensitivity component traits as the independent variables. The theoretical basis for this calculation lies in the theory known as the 'Ghost of species past' or the extinction filter hypothesis. This is the concept that past climatic, ecological and anthropogenic perturbations have to some extent filtered out species vulnerable to future climate change, by acting as an extinction filter (Balmford 1996). The central tenet of the extinction filter hypothesis is that those regions which biotas have experienced perturbations leading to extinctions of sensitive species during past warming (transition from glacial to inter-glacial since the last glacial maximum) now appear less vulnerable to future similar perturbations (Turvey and Fritz 2011).

Sensitivity and Past Exposure

The component traits of Sensitivity were found to weakly correlate with species' past exposure (r^2=0.155, adjusted r^2 =0.113, p=0.00), indicating that past climate change as characterised here has left a weak statistically-significant fingerprint on species assemblages, influencing the species composition by the degree of exposure to past climate change. To put the past exposure- sensitivity regression r^2 value in context, in a meta-analysis of regression-based literature Moller & Jennions (2002) found that the average reported r^2 value for ecological studies is 5.42% with 80% (n=43) of studies reviewed reporting r^2 values below r^2=0.10. Thus, the past exposure –sensitivity regression value of r^2=0.15 is within the bounds of expected values determined across a range of ecological regression analyses.

Although, theoretically it should be possible to explain 100% of the variance in data, the randomness and noise associated with the complexity of ecological systems and related ecological data considerably reduces this likelihood (Moller & Jennions 2002). This complexity is rooted in the ecological reality that 1) adaptation is not perfect or consistent and is dependent on selection pressures; 2) the "random" aspect introduced by unpredictable physical properties of the environment; 3) species responses to change are individualistic balanced across many different factors (e.g. size, age, predation risk); 4) accurate measurement is complicated due to geographical and temporal variation; and, 5) an organisms evolutionary past affects its ability to adapt (Maynard Smith 1978 optimization theory).

What evidence is there for the 'Ghost of species past' theory?

A central principal relating to the extinction filter hypothesis is that regions where biotas have experienced perturbations leading to extinctions of sensitive species during past warming should appear less Sensitive than other biotas (Turvey and Fritz 2011). However, species occurring beyond the extent of the glaciated regions continued to thrive during the last ice age, and therefore Sensitive species remain in the biota (Davis and Shaw 2001).

There is a strong latitudinal gradient in velocity of past climate change being of greater intensity away from the tropics (Davies and Buckley 2011). This is apparent in the

LHTd213 where there is a significant difference between past exposure for temperate compared to tropical regions (ANOVA F(1,212)=5.117, *p*=0.02). Thus, temperate biotas, particularly those from glaciated regions, should appear less Sensitive than their tropical counterparts. In comparing the impact of past exposure in determining individual species Sensitivities across the realms, accounting for Order, past exposure was found to be significant in describing the degree to which species are Sensitive in the temperate realm (ANCOVA, F=1,125)=4.41, *p*=0.03) but not the tropical realm (ANCOVA, F(1,86)=2.924, *p*=0.74). It is possible that significance is only found between past exposure and sensitivity for the temperate zone due to the better representation of species in the region.

3.4.4 Which Mammal species are identified as being sensitive?

This research sought to identify those species most Sensitive to climate change, but more importantly the Orders and their composite traits associated with Sensitivity. As discussed previously, several attributes have been associated with species sensitivity and resilience within the literature (Williams *et al.* 2008; Isaac *et al.* 2009; Dawson *et al.* 2011). This section attends more closely to those species which are most Sensitive, and whether the hypothesised trends relating to Sensitivity and, the r-K continuum, body size (Koch and Barnosky 2006) and range-size (Davies and Buckley 2011) are upheld in the LHTd.

Which Species are most sensitive?

This section examines the top 10% most Sensitive species to elucidate upon whether the Orders and traits identified as conferring Sensitivity are robust to closer scrutiny.

With regards to the principles of r-K theory and resilience theory the species amongst the top 10% (n=21) most Sensitive species in the LHTd would be expected to be dominated by the *K-selected* Orders identified previously, the Artiodactyla, the Cingulata, the Hyracoidea, the Perissodactyla, Primates, and those species of the Carnivora demonstrating *k*-traits. As hypothesised there are 15 representatives of *K-selected* Orders in the top 10% most Sensitive species. These include two Artiodactyla, five Primates and 5 Carnivora and a single member of each of the remaining *K-selected* Orders. However, the final six species which make up the 10% most Sensitive species are from the *r-selected* Order Rodentia, and include 4 species of squirrel, the Coypu (*Myocastor coypu*) and the Capybara (*Hydrochoerus hyrochaeris*).

The Tufted Capuchin (*Cebus apella)* is the most Sensitive species (Sensitivity=14.01), overall, with four of the five primates (*Alouatta seniculus, Ateles paniscus*, *Cebus olivaceus*), appearing in the top 10 most Sensitive species. The final six include the brown bear (*Ursus arctos*), red deer (*Cervus elaphus*), Raccoon (*Procyon lotor*), Gray fox (*Urocyon cinereoargenteus*) and the grey squirrel (*Sciurus carolinensis*) and Copyu (*Myocastor coypu*). As expected the Sensitive species belonging to the *K- selected* Orders are characterized by 'slow' traits, with individual values predominantly in the upper quartile, particularly with regards to the reproductive traits. Sensitivity across the Rodentia species and Eulipotyphla (European Hedgehog *Erinaceus europea*) is less easy to characterize. Across the six species of Rodentia, Sensitivity is relatable to above median scores across the reproductive traits, with the exception of litter size. There is little consistency with most species having above median scores for combinations of 2-3 of these traits. The Hedgehogs combination of a long life span and restricted habitat breadth may explain its high Sensitivity value (Sensitivity=12.61). Thus, Sensitivity can be said to be most strongly related to the reproductive components identified in the PCAf.

Does Body size play a role in determining sensitivity?

Large mammals are hypothesized to be more Sensitive to future climate change (Davies *et al.* 2009). In past episodes of climate warming large-bodied Mammals were disproportionately affected, experiencing high levels of extinction (Koch and Barnosky 2006). In fact, Turvey and Fritz (2011), found evidence during the late Quaternary period for the successive removal of large-bodied species in extinction-prone areas, which they identified as signalling the existence of an extinction filter. Those large-bodied Mammals which survived are therefore hypothesised to be more sensitive to future climate change than their smaller compatriots. Large Mammals (3kg and above,(Cardillo *et al.* 2008) account for 79 of the total species represented in the LHTd.

Species with a larger body mass are significantly more Sensitive than those below 3kg (F(204,2)=35.381,*p*=0.00, η²=0.148, (GLM accounting for Order)).

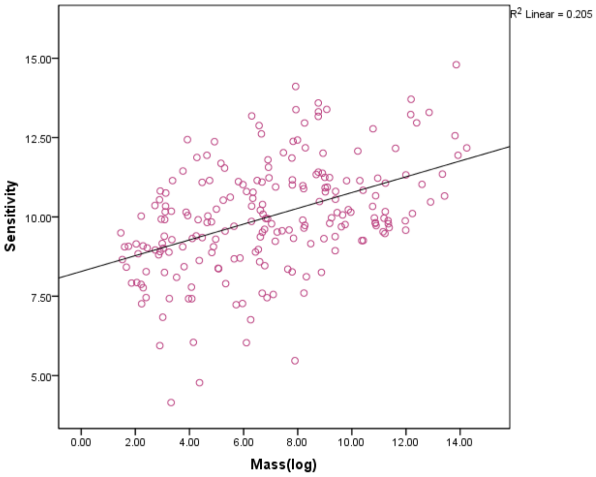


Figure 3.13.7 Biplot Sensitivity versus Body Mass (log.g)

To explore whether a correlation exists between body mass (log grams) and Sensitivity in the LHTd213 a biplot with regression line was plotted (Figure 3.13). There is a moderate correlation between body size and Sensitivity (r^2 =0.20).

Are Range-restricted Species more sensitive?

Range-restricted species are thought to be more at risk from extinction(Cardillo *et al.* 2008; Fritz *et al.* 2009). An ANOVA of range-restricted species (<250,000km ^{2} (Caballos 2006), n=8) Sensitivity against wide ranging species found that the relationship was non-significant (F=(1,204)=0.859, *p*=0.355). Distribution size is not included in the Sensitivity measure to avoid double-counting in future chapters in the assessment of Vulnerability, which may account for the lack of a relationship between Sensitivity and range size. However, this may also be explained by the lack of a suitable number of records for comparison.

Endemicity and Sensitivity

In the Sensitivity components endemicity negatively correlates with species climate niche, suggesting that endemic species have specialist habitat requirements. This would lead to the assumption that endemic species are likely to be more Sensitive, a hypothesis supported in the literature with regards to extinction risk (Purvis *et al.* 2000; Thomas *et al.* 2004).

There are 11 Endemic species represented in the LHTd213, five rodents, four bats, a single carnivore, a primate and a possum, none of which occur in the top 10% of Sensitive species. A significant difference was found between Sensitivity values for Endemic and Non-Endemic species, when accounting for Order (ANCOVA, F(1,204)=65.08, p=0.00, η^2=0.24). The relationship described, however, goes against what is expected with each of the endemic species Sensitivity being within the lower quartile of values for their specific Orders. This might be explained by the fact that these endemic species are all *r*-selected and thus conferred greater resilience to disturbances. Also, none of these species are range-restricted, which is largely the case when dealing with endemics (Purvis *et al.* 2000). Thus, because of the limited number of species listed as endemics in this database it is better not to place too much emphasis on this result.

3.4.5 Justification of Methods and Caveats

As discussed the measure of Sensitivity represented in this chapter successfully represents those trends identified in the literature as determining species sensitivity (Bielby *et al.* 2007; Williams *et al.* 2008; Isaac *et al.* 2009; Foden *et al.* 2013). However, it is important to recognise the Sensitivity measures' limitations.

Justifying Selection of the Vulnerability Framework

There are several Vulnerability Frameworks in the literature each of which could have formed the basis of this research (Williams *et al.* 2008; Chin *et al.* 2010; Summers *et al.* 2012; Berry *et al.* 2013; Foden *et al.* 2013). The Williams *et al* (2008) framework was chosen on the basis of discussions with members of the wider team responsible for the framework's design and Wallace Initiative members at the Centre for Tropical Biodiversity and Climate Change, James Cook University (van der Wal and Welbergen pers.comm.). These discussions revealed the utility of using the William's *et al* (2008)

Vulnerability framework to determine the impact of climate change on species distributions using the Wallace Initiative exposure data and through the development of a Sensitivity component. At this juncture in early 2010 previous species climate risk assessments (Fussel and Klein 2006; Harley *et al.* 2006) had focused on spatial and temporal risk to specific species and their applicability to other species groups was low (Chin *et al.* 2010).

Caveats associated with Global Biodiversity Analyses

This study recognises the common caveats associated with any global study investigating biodiversity patterns, including i) the misidentification of specimens; ii) outdated taxonomy and faulty geo-referencing (Soberón and Peterson 2004), and steps were undertaken to reduce uncertainty associated with these caveats. The misidentification of specimens is ruled out of the species life history traits data in the creation of PanTHERIA by the calculation of mean values over multiple records for each species and by comparison with expert knowledge (Jones *et al.* 2009). With regards to the taxonomy issue in the preparation of the LHTd database, species records were updated to represent the most recent taxonomy available for mammals (Wilson and Reeder 2005). 'Climate niche breadth' is the sole LHTd variable for which geo-referencing has an important role in its definition because its calculation requires the use of species occurrence data. To reduce the issue of faulty geo-referencing the occurrence data used in this study underwent a rigorous cleaning procedure which removed records which were not geo-referenced and, further, those outside the recognised extent of the species distribution (more details on this cleaning process are available in the Appendix concerning the Wallace Initiative Model).

Caveats associated the Sensitivity measure

Uncertainty connected to the measures' representation of Sensitive traits

There are several factors outlined as contributing to a species' Sensitivity in Williams *et al*'s (2008) framework of Vulnerability. As discussed, the Sensitivity measure successfully accounts for the life history traits and climatic tolerances recognised as determining a species Sensitivity. It also explores the influence of phylogeographic diversity in determining Sensitivity examining variation in Sensitivity within Orders and major realms.

However, within the calculation of the Sensitivity measure several factors remain absent. These include genetic diversity, plasticity, population dynamics and minimum viable population, dispersal potential. With regards to the absence of genetic diversity and plasticity data in the Sensitivity measure, there is scant information available because both are exceptionally difficult to quantify, with few species having had their genetic diversity characterized or plastic responses observed (Williams *et al* 2008). Williams *et al* (2008) recommend using a proxy to make informed estimates of the contribution of genetic diversity to Sensitivity, by using knowledge on species range and population size because restricted range species with small populations are predicted to have a low capacity for adaptation to environmental change – although this method comes with its own associate caveats. Although, dispersal potential is recognised as a determinant of Sensitivity is was omitted from the creation of the Sensitivity measure to avoid double-counting in the final measure of Vulnerability, as it is a composite factor in the creation of the Exposure measure. Population dynamics and minimum viable population data were not characterized in this analysis because data was unavailable for a sufficient number of species within the databases complicating the calculation of the Sensitivity measure.

Uncertainty associated with the measures calculation

The calculation of the Sensitivity measure is carried out using PCA, PCA is often used and considered to be 'elementary,' although there a several potential caveats associated with its use (Budaev 2010). One potential caveat is that PCA is able to produce 'meaningful' results from deficient data, thus, the input variables need to be initially assessed as to relevance to the biological pattern you are seeking before the PCA is run (Budaev 2010). To avoid this major flaw before the LHTd variables were input into the PCA each was assessed as to its relevancy in determining species' Sensitivity using the literature. Further, the output from the PCAf was compared with accepted ecological principles to check the degree to which it is robust. Selection of the appropriate rotation, the determination of which loadings should be considered in the interpretation of the components, and the appropriate minimum sample size can all introduce uncertainty in the analysis when using the default PCA model (Budaev 2010). To make sure the Sensitivity components identified were robust each of these stages was carefully considered and the most appropriate methods chosen as recommended in the literature (Smith 2002; Anglim 2009; Tabachnick and Fidell 2012).

The caveats recognised in this section need to be acknowledged when applying knowledge gained through the creation of the Sensitivity values, particularly with relevance to the calculation of species overall Vulnerability in future chapters.

3.4.6 Conclusions

The analysis above reveals which life history and ecological traits are important in shaping species Sensitivity to future climate change. In doing so it has identified those species predestined to be sensitive to future climate change by their innate life history and ecological traits.

The results relating to life history characteristics and Order presented here closely identify with those found by Dobson and Madan (2007) in their paper considering Fast and Slow life histories of Mammals. They investigated where Orders lined up along the fast-slow continuum with regards to reproduction and survival traits using PCA. They positioned each Order along the continuum according to their average rank across the traits. The Artiodactyla had the slowest life histories followed by the Carnivora, Rodents, Primates and finally the Lagomorpha with the fastest life histories. In this study the Most Sensitive Order are the Primates followed by the Carnivora, Artiodactyla and Rodentia with the Least Sensitive identified as the Lagomorpha. The Sensitivity measure evidently takes into account a wider diversity of traits and as such is more complex than the ranking of survival and reproduction traits which explain to some extent these differences. Accounting solely for reproduction-survival traits the Artiodactyla switch position with the Carnivora but the position of the Primates remains at odds with Primate in this analysis consistently exhibiting ‘slow’ life history traits. However, in a later study looking in more detail at mammal life histories Dobson and Madan (2008) did find that Primates exhibited low fertility, long gestation periods and long time to age at maturity, acknowledged ‘slow traits’ and in agreement with the trends identified in this study. This level of agreement in the literature indicates that the Sensitivity measure is successfully defining those characteristics believed to predetermine the level of innate sensitivity individual species encompass.

The cluster analysis shows that mammal species individual Sensitivities do not cluster rigidly by Order, this conclusion finds agreement in the literature (Bielby *et al.* 2007; Dobson and Oli 2007, 2008; Lyons *et al.* 2010). Lyons *et al.* (2010) suggest although similarities exist between Orders of mammals and their species individual trait sets strict sets of traits do not exist. Dobson and Madan (2007) found wide variation in life history characteristics across Orders, particularly across the Rodentia. They observed that although the Lagomorpha were as the Order containing the species with the fastest life histories, there was wide variation across the Lagomorphs with the European Hare (*Lepus europaeus*) having life history characteristics more akin to those identified as 'slow'. This finding is reflected in the analysis of trait variation across clusters where the cluster containing the Lagomorpha shows very wide variation across the reproductive traits particularly litter size. This variation complicates assigning a Sensitivity classification to species for which we have limited information. Therefore, to further the utility of the Sensitivity measure a concerted effort to collect missing trait data is required. It is recognised that the factors limiting a species' range shifts are both complex and multifaceted (Parmesan 2005; Lyons *et al.* 2010) consequently it is not surprising that this study observed only a weak correlation between sensitivity and the past velocity of climate change. In a similar test Lyons *et al* (2010) investigated the impact of phylogeny, life-history traits, body size and topographic heterogeneity on species range shifts during the last megafaunal extinction. As in this study they also found limited predictive ability when assessing the relationship between ecological and life history traits and change in species range size. However, Lyons *et al* (2010) observed that of the life history traits they explored the majority had a significant but weakly positive correlation with the distance species shifted in the past. Their results are in agreement with those presented in this research that life-history traits played a role in determining past change in species distributions.

There are no previous studies which have sought to predict mammal sensitivity to climate change for comparison, however, the studies discussed here have examined traits identified in the literature as relevant to sensitivity (Williams *et al.* 2008; Isaac *et* *al.* 2009; Dawson *et al.* 2011) and touched on factors identified as relevant to the 'Ghosts of species past' theory central to the validation of the Sensitivity measure (Lütolf *et al.* 2006; Turvey and Fritz 2011). Comparison with the literature and the agreement found provides a strengthened argument for the use of the Sensitivity measurement developed. The novel measure described here provides a firm foundation stone upon which to base investigations of species vulnerability to future climate change.

4 Calculating Species Future Vulnerability to Climate Change

4.1 Research Context

The IUCN Red list currently lists 21% of mammals as threatened by extinction (IUCN 2013). In order to avoid mass numbers of extinctions better understanding is needed into the threats which species are exposed to, and species unique susceptibility to individual threats (Fritz *et al.* 2009).

It is broadly agreed that whilst some species will be disproportionately affected by climate change others have the potential to thrive (Parmesan and Yohe 2003; Thomas *et al.* 2004). This study seeks to assess the impact of climate change on species through the estimation of each species Vulnerability to future climate change.

This study will concentrate on the analysis of mammal Vulnerability because of the wealth of knowledge and accompanying data, Mammals are the only species-rich taxon for which there is a species-level phylogeny, global maps of their distributions and in depth knowledge of biological traits (Fritz *et al.* 2009).

4.1.1 The Impact of Past Climate Change on Mammal Diversity

Past climatic change shaped current mammal communities (Blois *et al.* 2010). The current mammalian biota of the Northern biomes was strongly shaped during the climatic changes of the Quaternary which influenced individual species adaptations and distributions, as well as determining areas of endemicity (Lister 2004). It is unknown whether these fluctuations influenced mammal communities in other regions of the world, although there is evidence that at the beginning of the Quaternary the diversity of African mammals increased considerably indicating that disturbances occurring during this period may have kick-started diversification (Lister 2004).

At the close of the Late Quaternary, around 50,000 years ago, the mammalian megafauna (large-bodied mammals) of North America and Eurasia experienced a reduction in diversity of approximately 72% and 36% respectively (Lorenzen *et al.* 2011). These extinctions coincided with the most dramatic climatic changes of the

Quaternary suggesting that climate change was a major driving force, along with, to a lesser extent, anthropogenic stressors, in bringing about these large-scale losses (Blois *et al.* 2010; Lorenzen *et al.* 2011).

The small mammal community was not immune to the effects of past climatic change (Blois *et al.* 2010). Blois *et al* (2010) investigated the impact of climate change on small mammal populations in northern California at the end of the Pleistocene epoch (11,700 ya). They found that although no small mammal species went extinct, extant communities experienced declines in overall evenness and richness. These changes are reflected in modern North American mammalian communities being both depauperate in megafauna and small mammals (Blois *et al.* 2010).

4.1.2 **Mammals and Current and Future Climate Change**

In a reconstruction of temperatures over the past 1000 years warming in to 20th century far exceeds that expected with natural variability (van Vliet and Leemans, *et al* 2006). Under the SRES A1B scenario, commonly referred to as 'the business and usual' storyline (Pachauri and Reisinger 2007), future warming is projected to achieve rates of increase of 0.03°C/ yr (0.02-0.04) from 2000-2100 (Loarie *et al.* 2009). This rate of 3°C/ century is an order of magnitude faster than any rate found over the past millennia (0. 2°C /century). In a comparison of climate change in the 20th century with the most recent millennia of the late Holocene, the most relevant for exploring the likely uniqueness of future climate change, Jones and Mann (2004) found that 20th century climate change was the largest within any century of the past two millennia (0.6-0.9°C), this is compared with less than ±0.2°C for any other century during the period.

The degree to which species will survive or an ecosystem will persist under climate change will depend on each species' capacity to adapt as well as their respective innate resilience (Williams *et al.* 2008). A species' or individual's sensitivity to environmental change is governed by intrinsic factors which include their physiological tolerance limits, their ecological traits such as behaviour, and their inherent genetic diversity (Williams *et al.* 2008).

There is evidence that species have already used pre-existing flexibilities in responding to climate change, such as contraction to refugia, shifts in distribution, and shifts in habitat and microhabitat, shifts in seasonal and daily activities, acclimation, and changes in biotic interactions (Williams *et al.* 2008; Wiens *et al.* 2009). In a longitudinal study of small-mammal responses to global warming conducted in Yosemite National Park, California scientists found that half of the 28 species monitored exhibited upward changes in elevational limits (500m average) in response to an observed ~3°C increase in minimum temperatures (Moritz *et al.* 2008). Species with ranges at low elevations previously were found to have expanded their ranges upwards whereas high-elevation species ranges contracted with the effect of changing the community composition at mid- and high elevations (Moritz *et al.* 2008).

Leemans & Eickhout (2004) predict that with between 1 and 2°C warming most species, ecosystems and landscapes will have experienced a degree of climate change which will severely limit their adaptive capacity, manifesting in observable biodiversity declines. The likelihood that mammal species will shift and potentially expand their ranges to encompass novel climatically suitable areas will be constrained by a number of factors, such as dispersal capability, biotic interactions, behavioural patterns, natural barriers and habitat fragmentation(Maiorano *et al.* 2011).

Dispersal capability

Dispersal capacity is likely to be a considerable barrier to mammal species' ability to track projected changes in suitable climates (Schloss *et al.* 2012). Dispersal capacity is identified as a key factor in determining species survival capacity (Guisan and Thuiller 2005; Walters *et al.* 2006; Lester *et al.* 2007; Williams *et al.* 2008). The importance of dispersal as an adaptation mechanism is evidenced by past climatic change when oscillations in glacial maxima and minima in the high latitudes and accompanying fluctuations in temperature during the Quaternary favoured recolonisation by good dispersers able to exploit competition-free space during glacial minima (Davies *et al.* 2009). These mammal species tended to have wide habitat breadths and be pre-disposed to occupying large geographic ranges (Davies *et al.* 2009).

Schloss *et al* (2011) examined the capacity of Western hemisphere mammal species to disperse and compared this with the projected velocities of future climate change finding that on average 9.2% of species at a given location may be unable to track suitable climates, rising to 39% in some locations. Schloss *et al* (2011) found that 87% of mammals species will experience some reduction in range size, 20% of these reductions were due to their inability to keep pace by dispersal not reduction in suitable climate space. The average reduction in range was 37%, although the primates were predicted to experience more severe range reductions of around 75% (Schloss *et al.* 2012). Many Artiodactyla and Carnivora species, conversely, were predicted to expand their current ranges (Schloss *et al.* 2012). The species of the tropical and subtropical forest of the western Amazon were found to be least likely to keep pace with 14.5% of species unable to track suitable climates (Schloss *et al.* 2012). Climate change is likely to outpace mammal species capacity to respond leaving many more species vulnerable to climate change than previously estimated (Schloss *et al.* 2012).

Biotic interactions

Biotic interactions are likely to be impacted as community structures are modified by climate change (Wiens and Graham 2005). Rapid climate change will initiate structural changes in the composition of small mammal communities and impact the overall functioning of the ecosystem of which these communities form a part (Blois *et al.* 2010). Based on their findings regarding the effect of past climatic change on small mammal communities Blois *et al* (2009) predict a further decrease in species richness accompanied by escalating species turnover and the localised growth of generalist species abundances to the detriment of specialists in communities with heightened susceptibility to disturbances.

Behavioural patterns

There are few observations of the impact of climate change on mammal phenology with the main body of evidence documenting changes in vertebrate phenology focusing on long-term studies of birds (Moyes *et al.* 2011). One such observation is detailed by Moyes *et al* (2011) who provide evidence for changes in several attributes of Red Deer phenology observed as part of a long-term study on the Isle of Rum, Scotland. They found that oestrus date and parturition date in females and antler cast and antler clean and rut start and end dates in males advanced by between 5 and 12 days across a 28 year period. These changes in phenology were linked to changes in climate warming which impacted the deer's directly by effecting their ability to thermoregulate and indirectly through increasing plant growth and food availability earlier in the season (Moyes *et al.* 2011). There are Mammals at all latitudes, even within the deep Tropics, which reproduce seasonally cued by foraging conditions, photoperiod or ambient temperature (Bronson 2009). Long-lived mammals' reproduction, from the highest latitudes to the mid-tropics, is commonly triggered by photoperiod the trigger for short-lived mammals is less clear but some desert and dry grassland species have been observed reproducing after seasonal rains (Bronson 2009). This reliance on environmental factors suggests that changes in climate will have a bearing on mammal reproduction particularly with long-lived species which are less able to adapt than smaller more fecund mammals such as rodents because of their dependence on photoperiod and slower adaptation potential (Bronson 2009).

Mammals are observed as being highly sensitive to temperature, despite being endothermic, suffering heat stress when temperatures reach extremes (Morueta-Holme *et al.* 2010). There are observations of mass mortality events following periods of extreme high temperatures, for example the mass mortality of Australian flying foxes caused by a prolonged period of hot extremes (Welbergen *et al.* 2008). Evidence from the past, in the form of the decline in range of the musk ox by 60% after the LGM, further illustrates the sensitivity of mammals to temperature (Lorenzen *et al.* 2011). Musk Ox are unable to endure high summer temperatures supported by the fact that the southern limit of their present range is determined by the 10°C summer isotherm (Lorenzen *et al.* 2011) .

Natural barriers and habitat fragmentation

Natural barriers and habitat fragmentation will limit the capacity for species to disperse through the landscape. Mairano *et al* (2011) identified mammal species of the Mediterranean peninsulas as being at particular risk from climate change due to the envisaged difficulty involved in species moving northwards due to east-west orientated mountains ranges such as the Alps and Pyrenees, the same is true of island species, many of which are endemic. Endemic mammal species are highly at risk because of their limited ability to disperse and track rapidly shifting suitable climate space (Morueta-Holme *et al.* 2010). An in-depth study of the impact of climate change on the Pyrenean desman's (*Galemys pyrenaicus*) sought first to identify the factors which determine its current distribution identifying dispersal ability in combination with water balance and mean summer temperature as the main factors (Morueta-Holme *et al.* 2010). This restricted mountain endemic is therefore likely to be highly sensitive to future shifts in suitable climate with future suitable space lying far beyond the species current distribution (Morueta-Holme *et al.* 2010).

There is inherent variability in the degree to which different sites and regions have and are predicted to experience exposure to climate change, in the magnitude, duration and the frequency of periods of favourable and unfavourable climates (Jackson *et al.* 2009). Thus, there is projected to be regional variation in the impacts of climate change. Warming is projected to be greatest on land with high northern latitudes experiencing the highest degree of warming (Solomon *et al.* 2007). Patterns of precipitation are also predicted to shift with high latitudes likely to experience and increase in precipitation, whilst subtropical land regions are likely to experience a decrease (IPCC 2007).

The likelihood that future climates, unprecedented within the range of current climates, will occur, so called non-analogue climates, is high (Williams and Jackson 2007). These novel climates are particularly prevalent at a regional scale, with scenarios exhibiting within region-variation outside the natural range of climates present or past encountered across the specific region (Williams, Jackson and Kutzbacht 2007). These future novel climates are reported to be warmer than any present climates, and accompanied by shifts in precipitation patterns (Williams and Jackson 2007). Regions likely to experience the majority of climate mismatches by 2100AD are identified as South America, Africa, India and the Indo-Pacific (Williams and Jackson 2007). Evidence from past climate change episodes suggest that these future novel climates are likely to promote novel communities (Williams and Jackson 2007).

Maiorano *et al* (2012) investigated the impact of future climate change on hotspots of mammal biodiversity across Europe finding that the species they host are likely to experience significant exposure to climate change alongside the appearance of novel climates. The hotspots predicted at risk of high exposure to extreme climates are concentrated in two sectors, southern and north-eastern Europe. These regions encapsulate in Southern Europe the highly biodiverse Mediterranean basin and surrounding mountain chains an important refuge for endemics and threatened species, and in north-east Europe the Boreal and Arctic bioregions and the Urals (Maiorano *et al.* 2012). High latitude mammal species in the Artic and subarctic have been predicted to be particularly at risk from future climate change, with temperate climates expanding northwards and tundra habitat contracting, however, Hof *et al* 2012 predict that climate change to 2080 will favour most European subarctic mammals, assuming full dispersal (Hof *et al.* 2012). Those species remaining at risk are cold-specialists and those unable to track shifting climate space due to limited or constrained dispersal ability (Hof *et al.* 2012). One potential reason for this comparative stability in mammal occurrences is the legacy of previous large climatic shifts in filtering out sensitive and range-restricted species and shaping the current mammal biota (Hof *et al.* 2012).

4.1.3 **Projecting Impacts of Future Climate Change upon Species**

Niche models, such as that used in the Wallace Initiative, provide a way of analysing the exposure of species distributions to the magnitude and rate of climate change projected under alternative emission scenarios. Climate change is a global phenomenon and as such its impacts are to be experienced by all species, although the degree to which individual species will be affected will vary greatly (Dawson *et al.* 2011). Quantifying this variation in exposure across regions requires the projection of future climates using climate models, known as General circulation models (GCMs). GCMs predict future climates using a series of algorithms representing different facets of the global climate. Thus, the projections of future species distributions (future suitable climate space) are dependent on the climate model and the scenario chosen to represent future climate change (Beaumont *et al.* 2008).

In creating projections of future climate change it is important to recognise that the further from the current climate projections move the less robust they become, this is because future climates may diverge profoundly from the present (Williams and Jackson 2007). This means that models seeking to predict changes in ecological phenomena, such as species distributions, accuracy will be undermined if projected onto future climates significantly different to the current (Williams and Jackson 2007).

4.1.4 **Objectives**

This chapter seeks to develop a measure of species Vulnerability to climate change by incorporating both a measure of species' innate Sensitivity and projected Exposure to climate change. This chapter employs the Sensitivity measure determined by life history and ecological traits developed in Chapter Three. Building on the work in Chapter Three it explores the potential impact of unmitigated climate change under the business-as-usual SRES A1B scenario of future climate change to determine the level of exposure that individual species are predicted to experience. Finally, this chapter combines both Sensitivity and Exposure measures into a Vulnerability score. This measure of Vulnerability is then explored across Orders and within Biogeographic realms and zones. These further analyses are undertaken to determine whether species belonging to a particular Order or biogeographic zone are more at risk from climate change. The result of these analyses will help to inform conservation planning in the light of future climate change.

This chapter will address the following specific research questions:

- To what degree will individual species be exposed to future climate change?
- How does the level of Exposure differ across taxonomic orders, species and biogeographic zones?
- What is the effect of combining knowledge on sensitivity and exposure into a single measure of Vulnerability in determining which species will be most at risk from future climate change?
- Are there Orders which are predicted to be more Vulnerable than others under future Climate change?

- Are there Biogeographic zones which possess more Vulnerable species than others under future climate change?

4.2 Methods

4.2.1 Mammal Sensitivity Data

Mammal Sensitivity scores were created for 213 species (Chapter Three), which represent those which had complete records for the full suite of 10 life history and ecological traits identified in the final Principal Components Analysis PCAf conducted in Chapter Three. These records represent 15 orders and 58 families. These data are extracted from the Life History Traits database LHTd created in the Chapter Three.

Sensitivity is scored by summing the factor scores created across the three components generated in using the Principal components analysis described in Chapter Three, the representative traits are listed in Table 3.8 with their individual loadings across the components.

4.2.2 Future Exposure Data

The term ‘Future exposure’ describes the predicted effect of climate change on a species’ future distribution. It is represented by the proportional change in a species distribution predicted to occur between the current predicted area and that predicted for 2080 and is termed Exposure^{R}, where the R indicates that it refers to the proportion of range remaining. Current and future distribution projections are output supplied by the Wallace Initiative. Future projections of species distribution were made using the global warming scenario ‘SRES A1B’ as defined in the IPCC AR4 report (Solomon *et al.* 2007).

The ‘SRES A1B’ (Pachauri and Reisinger 2007) storyline describes a world of rapid economic growth, where the global population peaks mid-century and there is rapid introduction of more efficient technologies. Global energy consumption is described as balanced between fossil-intensive and non-fossil energy sources (Pachauri and

Reisinger 2007). This scenario represents a temperature increase of 2.3°C (1.4°C-3.5°C) by 2080 relative to the temperature at 1990-1999 (Pachauri and Reisinger 2007).

Future Exposure: Projecting the Impact of Future Climate Change on Species

There are many stages in order for unique Exposure^R values to be calculated for each species. The process by which projections of species distributions were calculated under future climate change is addressed below and in further detail in Appendix 2: The Wallace Initiative and Species Distribution Modelling.

Input Data Preparation

Species distribution models require two inputs to run, the observed species distribution data and the explanatory environmental variables. In the case of the Wallace Initiative primary biodiversity data was sourced from the Global Biodiversity Information Facility (GBIF, (GBIF 2013)) and environmental variables were projections from projected a suite of general circulation models (GCMs) (Warren *et al.* 2013).

Before the data's use in the Wallace Initiative it underwent computerised cleaning process consisting of three levels; 1) removal of records with no location data or which did not fall on a land area; 2) removal of occurrences which did not match the reported country of origin; 3) removal of points considered as outliers based on the species niche requirements (Warren *et al.* 2013) .

A suite of eight environmental variables was used in the Wallace Initiative from downscaled climate projections created using an ensemble of seven general circulation models representing six alternative greenhouse gas emission scenarios, and at 0.5°x 0.5° resolution (Warren *et al.* 2013). The environmental variables include: annual mean temperature, temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month, annual mean rainfall, rainfall seasonality, rainfall of the wettest quarter and rainfall of the driest quarter. These environmental variables were selected as they are recognised as capturing the widest range of variance across a range of species climatic niches (Warren *et al* 2013).

The model used to predict current and future species distributions is the presence-only method Maxent (Warren *et al.* 2013). The principle of maximum entropy is that it 'agrees with everything that is known [i.e. that inferred from the environmental conditions at the occurrence localities], but carefully avoiding anything that is not known,' (Jaynes 1991; Phillips *et al.* 2006). The model Maxent seeks to maximise its predictive capacity of species distributions by reducing uncertainty associated with the environmental variables. Thus, in Maxent's case, entropy is defined as a measure of the uncertainty connected with a random variable (Phillips *et al.* 2006). The maximum entropy probability distribution describes the modelled species distribution which exhibits the lowest entropy in synchrony with the maximised distribution (Phillips *et al.* 2006). The Maxent default settings were unaltered because they have already undergone optimization routines for a broad range of species, globally (Phillips *et al.* 2006; Phillips and Dudik 2008). The impact of altering settings within the Maxent model is further discussed in a case study included as part of Appendix Two: The Wallace Initiative and Species Distribution Modelling Techniques*.*

Maxent is considered to be one of the most robust forms of presence-only species distribution models currently available (Elith *et al.* 2011). Maxent has been shown to combine excellent predictive ability and moderate sample sensitivity (Wisz *et al.* 2008). Maxent's consistent performance across a range of sample sizes was highlighted by Wisz et al (2008), who found that it outperformed a number of other models at low sample sizes (10 unique points) and was bested by only one other model at high (100 points) and intermediate (30 points) sample sizes. Maxent has also been assessed as robust to a moderate degree of error implicit in the locational data, able to produce meaningful projections of the species distribution (Graham *et al.* 2008). Maxent's good performance may be a function of the generative rather than discriminative approach it uses, modelling the species distributions directly. This generative approach may go some way to explaining its success with small amounts of training data, as generative methods have been found to outperform discriminative (regression) models at small sample sizes (Phillips and Dudik 2008). Phillips and Dudik (2008), state that Maxent may outperform regression methods such as GAMs and GLMs when using presence-only data because regression-based methods use background data taken from across the model space to use as absence data when it may be contaminated with presences, contaminating the control.

Ensemble modelling, where a number of species distribution models are run simultaneously and the output assembled, has been recommended by the literature to reduce biological uncertainty (Araujo and New 2007; Jones *et al.* 2013). This is because bringing together several model outputs helps quantify variability in projections capturing consistency as well as structural uncertainty in projections (Jones *et al.* 2013). In a test of uncertainty in ensemble models biological uncertainty was found to contribute the largest degree of variability across models, with one third to a half of all uncertainty relatable to statistical method used (Buisson *et al.* 2010). The major parts of remaining uncertainty related to the GCM and Emission scenario used. In this case running an ensemble was outside the scope of the analysis and the single model Maxent was selected due to its reputation as one of the best performing simulators of species distributions (Elith *et al.* 2011).

Prediction of species current distribution

The model is used initially to predict the species current distributions using presence data. The first procedure implemented trains the model; this stage estimates a probabilistic distribution of the species current geographic distribution using observed data points from GBIF (Warren *et al.* 2013). This process derives the relationship between the species' presences and the environmental variables. The higher spatial resolution 10 arc-minutes Worldclim environmental indices (Hijmans *et al.* 2005) were employed in this initial stage so as not to lose information about species environmental requirements (Warren *et al.* 2013). This is particularly relevant when modelling species with small distributions, for instance an endemic species occurrence points may be clustered with a 0.5°X0.5° cell, but represent a series of differing environmental conditions (van der Wal, pers. comm.). The variable sets are illustrated in Table 4.1 Environmental Variable Sets

. Only taxa with at least 10 geographically unique observation points were modelled, all eight environmental variables were utilised as driving variables for species with over 40 unique points (Warren *et al.* 2013). A subset of four (including Annual mean temperature, Temperature seasonality, Total annual rainfall and rainfall seasonality) were used for species with 10-39 observations (Warren *et al.* 2013). The four variable set is used in instances when fewer than 40 occurrence points are available to avoid overfitting the model resulting in an overly constrained prediction of the species suitable climate space. These variable sets were selected because they are thought to best represent the variables which drive species distributions across a broad range of taxa (van der Wal, pers. comm.). The effect of varying both the environmental variables selected and the number of environmental variables included in the model in determining a species environmental niche is further investigated in the Appendix Two: The Wallace Initiative and Species Distribution Modelling Techniques.

Environmental Variables	**Code**	**8 Variables**	**4 Variables**
Annual Mean Temperature	BIO1	▨	▨
Temperature Seasonality	BIO4	▨	▨
Max Temperature of Warmest Month	BIO5	▨	
Min Temperature of Coldest Month	BIO6	▨	
Annual Mean Precipitation	BIO12	▨	▨
Precipitation Seasonality	BIO15	▨	▨
Precipitation of Wettest Quarter	BIO16	▨	
Precipitation of Driest Quarter	BIO17	▨	

Table 4.1 Environmental Variable Sets

The second procedure calculates the species actual distribution for all global land areas using the derived species-environment relationship (Warren *et al.* 2013). These predicted 'current' distributions are constrained by two factors; “a 2000km buffer around the occurrence records including any oceanic islands within it, and the limits of the specie's biogeographic region” as defined by Olson *et al* (2001) (Warren *et al.* 2013). The sizeable 2000km buffer is used to allow for the likely paucity of the GBIF data (Warren *et al.* 2013). It is acknowledged that the application of such a large 2000km buffer could result in overestimation of species’ current distributions, particularly in the case of more localised species, however, when projecting in to the future it prevents the model predicting dispersal into areas already occupied by the species current distribution (Warren *et al.* 2013). The biogeographic zones are listed as Palearctic, Nearctic, Afrotropical, Neotropical, Australasia, Indo-Malaya, Oceania and Antarctic (Olson *et al.* 2001). Implementation of the zonal buffer, for example, prevented European species being predicted in North America which is likely due to the similarity in climatic conditions (Warren *et al.* 2013). The predicted distribution is thus constrained to climatically suitable habitats within the buffered region (Warren *et al.* 2013).

Projection of species future distribution

During the modelling process to predict the species current distribution the environmental characteristics of the species niche are determined. This unique combination of environmental features is inputted as the basis for projecting the species future distribution under the SRES A1B scenario. The Maxent model then searches across the projected climate landscape to find conditions which closely match those determined by the species current location in the climatescape (Phillips and Dudik 2008). In the creation of the projections each model was run for ten cross-validated runs to reduce uncertainty in Maxent's prediction accuracy (Warren *et al.* 2013).

To determine a species potential climate space Maxent uses the environmental and location information provided to estimate a probability distribution across the study area which satisfies a set of constraints determined by the occurrence data (Phillips *et al.* 2006). These constraints are imposed across the environmental predictor variables and represent the mean value and associated confidence interval as determined by the mean over the presences (Guisan *et al.* 2007). The model by probabilistic reasoning then chooses from the manifold probability distributions satisfying the set of constraints, which maximises entropy (i.e. that which is closest to uniform) (Phillips *et al.* 2006). By choosing the distribution which displays maximum entropy the model avoids placing any unfounded constraints on the final predicted distribution (Pearson 2007a).

Maxent is similar to logistic regression in that it weights each input variable (environmental variable) by a constant (Hernandez *et al.* 2006), creating Features. The model undergoes an iterative process, starting with a uniform probability distribution; it systematically alters the weighted variables until the likelihood of the occurrence in the dataset is maximised (Hernandez *et al.* 2006). That probability distribution (the modelled potential species distribution) which best satisfies the environmental constraints initially imposed by the occurrence data of the species, whilst representing the greatest distribution range (Phillips *et al.* 2006). The output is deterministic because the Maxent algorithm does not use randomness meaning that the resulting output will always be the same given the same starting conditions (Hernandez *et al.* 2006).

The future scenarios of climate change were created for use in the Wallace Initiative projections using CIAS (Community Integrated Assessment System, Warren *et al* 2008) which brings together projections from several Global Circulation Models (GCMs) climate projections. The GCMs include the UKMOHadCM3, CCCMA-CGCM3.1, IPSL-CM4, MPI-ECHAM5, UKMO-HadGEM1, CSIROMk3.0, and NCAR-CCSM3.0. Individual predictions of future distributions are created under each of these GCMs. The use of a suite of GCMs allows the exploration of uncertainty associated with the projection of future climate change (Beaumont *et al.* 2008). The Appendix Visualising Climate change makes a detailed comparison of projections of future annual mean temperature and annual mean precipitation for the SRES scenarios under each of the seven GCMs.

These projections of future species distributions are constrained by the species' realistic dispersal capacity. In the case of mammals the rate of dispersal is set at 1.5km/yr equivalent to 150km in 100 years and 120km over the period 2000-2080 for which the models are run (Warren *et al* 2013). This is an average rate of dispersal and across the taxa it is likely that some species will surpass this rate and others fall below it. Dispersal in this case is defined as the 'average long-term shift of an entire species' range taking into account potential repeated colonization and extinction events until a species' entire range catches up with the new 'environmental space'' (Warren *et al.* 2013). This measure of average yearly dispersal distance was arrived at by consultation with the existing literature on mammal dispersal capacities (Warren *et al* 2013). The dispersal scenario was applied in the form of a buffer around the current distribution with dispersal only able to occur over contiguous land areas within the same biogeographic zone. The period over which model simulations are created is restricted to 2080, although projections were available to 2100, because the further from the current climate projections move the less robust they become (Williams and Jackson 2007). This is because there is a likelihood that future climates will diverge profoundly from the present (Williams and Jackson 2007).

Although in using a suite of GCMs to project future climate reduces uncertainty surrounding future climates and climate change biological uncertainty remains uncharacterised. As elaborated upon previously in this section biological uncertainty has been found to contribute a third to a half of all prediction uncertainty (Buisson *et al.* 2010). It is important therefore to view results of this analysis with this source of uncertainty in mind.

The method by which these projections are created is further detailed in Appendix 2: The Wallace Initiative and Species Distribution Modelling Techniques.

Calculation of Mean Distribution Across GCMs

The output provided includes maps of future distributions averaged across the seven GCMs. However, this chapter uses the estimations of a species' current and future distribution area for the full suite of GCMs measured in km^2. This allows the investigation of uncertainty across the GCMs as discussed in the Appendix: Visualising Climate Change.

To facilitate the calculation of Exposure^R for each species the mean prediction of future distribution area was calculated across the GCMs. The mean was calculated because it gives equal weight to each of the GCMs, calculating the mean is an accepted method for calculating the central tendency of the predictions when using an ensemble of projections (Thuiller *et al.* 2004; Araujo and New 2007; Pearson 2007b). To minimize the effect of outlying GCMs in skewing the mean the top and bottom projections were disregarded, and the mean was calculated across the 5 remaining GCMs. As Current distribution is estimated based on observed climate a single prediction of area is available and no further manipulation of the data was required.

Calculating the Future Exposure Value

To calculate this value for each of the species the following equation is employed; where $\boldsymbol{x}$ represents the proportion of the distribution remaining at 2080. The initial distributions are measured in km^2 where the Current distribution in km^2 equates to 1.

$$\boldsymbol{Exposure^R = \frac{Future\ Distribution\ (km^2)}{Current\ Distribution\ (km^2)} = \frac{x}{1}}$$

These proportions represent the proportion of current distributional extent remaining at 2080; a value of 1 indicates that the extent of the distribution remains stable at 2080. A value of over 1 indicates range expansion and below 1 range contraction. Therefore a proportion of 0.75 would indicate 75% of the species distribution size is stable. However, this is a measure of absolute distribution extent and is not geographically-founded. Despite this the distribution predicted at 2080 is constrained to be within the dispersal capacity of the species ruling out the inclusion of suitable habitat outside the species natural capacity to reach. The degree to which a species can expand its range is also constrained by the species' realistic dispersal capacity. This value of Exposure (Exposure^R) is used for ease of understanding in the figures in the Exploring Future Exposure section only (Section 4.3).

4.2.3 Creating a Composite score of Vulnerability

The further assessment of species vulnerability required the creation of a composite score to represent Vulnerability. Composite scoring is frequently used in Psychology experiments, and is a method by which multiple variables are combined to create a single score (Anglim 2009). In this instance the two variables for combination are Sensitivity and Exposure (Equation 1).

$$Vulnerability = f(Sensitivity + Exposure)$$

In order that the variables contributed equally to the final Vulnerability score the Sensitivity was normalized, scaling between 0 and 1, where 0 is least Sensitive and 1 is most Sensitive. This means that the highest Sensitivity score (S=14.70) when normalised is equal to 1. The normalization of the Sensitivity scores rescales the measure to be in the same order of magnitude as the Exposure measure. This process removes the influence of large standard deviations so that each is weighted equally (Anglim 2009).

The Exposure^{R} measure was re-calculated to describe proportion loss as opposed to proportion range remaining at 2080 for the calculation of the final Vulnerability score. The inverse of the score is used so that the Sensitivity and Exposure scores correlate positively, i.e. high Sensitivity is indicated by a high score and High Exposure likewise. This inversion of Exposure^{R} also means that species which are predicted to expand their distributions under climate change are indicated by a negative score. This value is known as Exposure^{L}, where the L stands for proportion loss. This is an important adjustment for the calculation of the Vulnerability score so that by the addition of the two measures high scores indicate High Vulnerability and low scores Low Vulnerability. Therefore the final Vulnerability equation is:

$$Vulnerability = (Sensitivity(N) + Exposure\ (Proportion\ loss)$$

Where the N indicates that the variable has been normalized. The resulting Vulnerability scores range from least Vulnerable (-0.385) to most Vulnerable (1.585). The highest possible Vulnerability score is Vulnerability=2, a combination Exposure loss=1 (indicating 100% loss of current distribution by 2080) and Sensitivity$_{\text{normalized}}$=1 (equivalent to Sensitivity=14.95). The Exposure^{L} value is used in all calculations considering Future Vulnerability.

4.2.4 **Assessing Vulnerability**

Vulnerability was assessed by plotting each species individual Sensitivity against the predicted level of Exposure^{L} they are projected to encounter under future climate change using scatterplots. Exposure^{L} represents range loss and is proportion of a species current climate space which is lost under Future climate change. This value is between -1 to 1, where 0 describes stable extent, 1 is 100% loss in suitable climate space and -1 is 100% gain. Where Exposure is mentioned in relation to Vulnerability it will always refer to Exposure^{L}. Sensitivity values are plotted on the y-axis and Exposure^{L} (proportion loss) at 2080 on the x-axis. These scatterplots are split into four quadrants, i) High Exposure, High Sensitivity, ii) High Exposure, Low Sensitivity, iii) Low

Exposure, High Sensitivity and iv) Low Exposure, Low Sensitivity. The quadrants are determined by quartiles calculated for the Sensitivity data and Exposure data. The threshold is determined using the lower quartile Sensitivity value (L.Q Sensitivity=9.01) above which species are classified as having High Sensitivity. As a novel measure of Sensitivity there is no empirical basis on which to select where the threshold should be set. Therefore the results should be considered as identifying relative rather than absolute Sensitivity indicating which species are at greatest risk due to their Sensitivity among those analysed only. A similar approach was used by Foden *et al* (2013) when in the absence of empirical evidence or expert-opinion the threshold determining the most vulnerable species under a specific trait is set to encompass the top 25% of values. The Exposure bound is set at the mean value of Exposure^L across the dataset. The ecological reasoning for this is that species projected to lose a significant part of their current distribution by 2080 are increasingly susceptible to future stochasticity in climate, such as extreme events, they are also more Vulnerable to changes in land-use and associated fragmentation of habitat (Warren *et al.* 2013).

Species falling within the highly sensitive and highly exposed quadrant are the most at risk and are thus labelled 'Highly Vulnerable'. Within the 'Highly Vulnerable' categorisation there are species labelled as 'Extremely Vulnerable' determined by the upper quartile values of Sensitivity and Exposure^L in the data. Species in the Low Exposure, Highly Sensitive quadrant are at high latent risk, so are termed 'Moderately Vulnerable'. Those species in the High Exposure, Low Sensitivity quadrant are likely to persist under climate change and are labelled 'Lowly Vulnerable', because they are of least concern although they need to be monitored. Species in the low Exposure and low Sensitivity risk are labelled as 'Least Concern'.

4.2.5 **Vulnerability across Orders**

Exploration of Vulnerability within the Orders was undertaken to determine whether particular Orders are more vulnerable than their constituent species within the Mammalia. The taxonomy used is after Beck et al (2006) for the placental mammals, the Eutheria. However, because fully marine species were excluded from the analysis the Order Cetartiodactyla is again split into Cetacea (the Whales) and Artiodactyla (even-toed ungulates) to bring clarity to what is being modelled and investigated. Marine species the Walrus (*Odobenus rosmarus*), two species of seal and two species of sea lion remain in the LHTd because they colonise terrestrial habitats for at least part of their lifecycles. The taxonomy for the Marsupials (Infraclass Marsupalia) adopts the taxonomy developed by Wilson and Reeder (2005). The full taxonomy is presented in the supplementary material under Taxonomy.

Vulnerability is explored at the taxonomic level of Order to highlight the degree of variation in Vulnerability across the Mammalia. Life history traits, particularly reproductive traits, which contribute significantly to the Sensitivity measure, are theorized to be conserved above the family level (Bielby *et al.* 2007). In concert with this reasoning because of the limited number of records within the LHTd213 family level analysis is not meaningful for Orders with families represented by single species.

4.2.6 **Vulnerability by Biogeographic Realms and Zones**

To observe the impact of future climate change on species originating in differing climatic zones the species data were split along the lines of biogeographic realms, tropical or temperate and biogeographic zones. Species were extracted from the LHTd213 dependent on biogeographic realms and subsequently plotted as scatterplots with Exposure^{L} on the x-axis and Sensitivity on the y-axis.

Biogeographic zones were first envisioned by Wallace in 1876 (Wallace 1876). Biogeographic zones are divided along evolutionary history lines and thus take account of the common ancestry of the species assemblages contained within (Holt *et al.* 2013). There are several schemes of biogeographic or zoogeographic zones proposed (Wallace 1876; Olson *et al.* 2001; Holt *et al.* 2013).

Olson et al (2001) propose eight overarching biogeographic zones, an aggregation of those previously defined in the literature by Pielou (1979) and Udvardy (1975) (Figure 4.1). Udvardy (1975) delineated biogeographic realms on the basis of unifying features of geography and biodiversity.

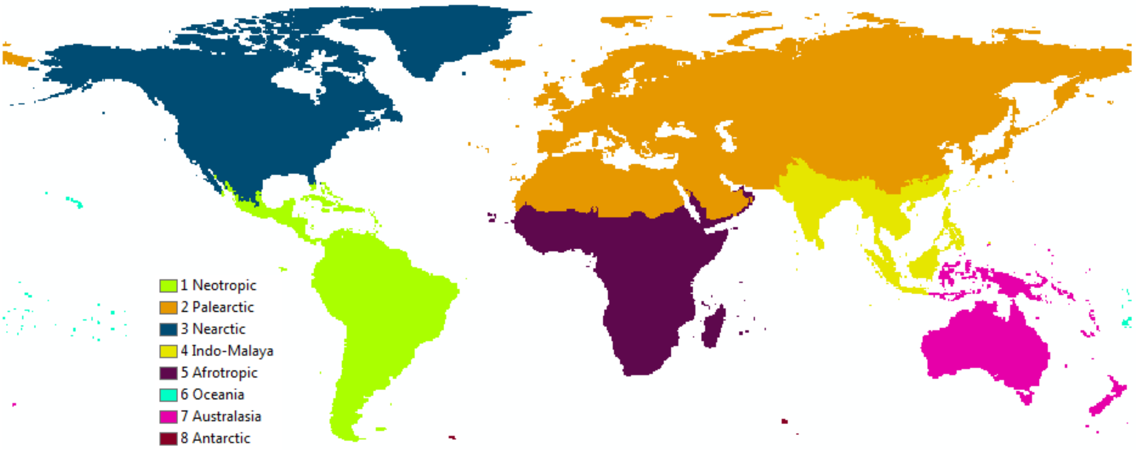


Figure 4.1 Biogeographic Zones as determined by (Olson *et al.* 2001)**.** Antarctica is not shown.

Holt *et al*,(2013) proposed an updated version of Wallace's biogeographic regions in which they used phylogenetic data to describe species evolutionary relationships resulting in the definition of 11 zones (Figure 4.2). Antarctica was not included in Holt *et al*'s(2013) analyses but is labelled in Figure 4.2, in reference to the zones described in the zonal statistic (SDMTools, VanDerWal, Falconi, Januchowski, Shoo, & Storlie, 2012) run subsequently.

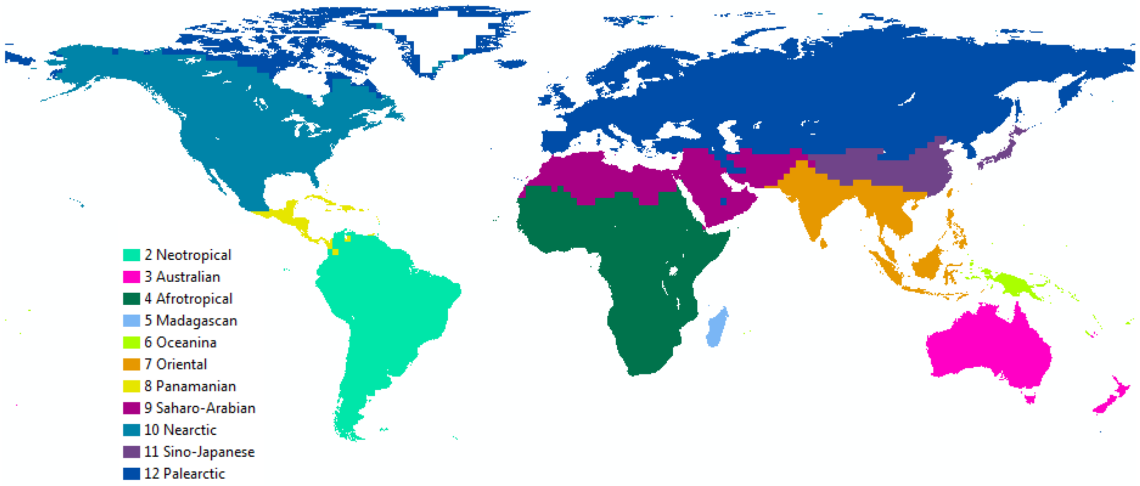


Figure 4.2 The 11 Biogeographic Zones as defined by Holt et al, (2013) with each zones associated number in LHTd. (Antarctic is not shown)

Due to the restricted number of mammal records in the LHTd213 the number of biogeographic zones investigated falls from 11 (excluding Antarctica) to seven, the Neotropical, the Nearctic, the Palearctic, Saharo-Arabian, the Oriental, the Afrotropical and the Australian zone. To avoid double-counting species which appeared in more than one zone within categorized in the zone in which their distribution is most dominant. There were no records for species unique to the Panamanian, Sino-Japanese, Oceania or Madagascan zone and therefore they were dropped from the analysis.

4.3 Results

4.3.1 Exploring Future Exposure across the Full Dataset

This section explores the degree to which Mammal species, represented in both the LHTd and the LHTd213, are projected to be exposed to future climate change. It examines differences in Exposure^R among the Orders, between the Tropical and Temperate Realms and the Biogeographic zones. Within this section on Exposure, the Exposure value referred to is always Exposure^R, proportion range remaining. This value is used because its scale is more intuitive than Exposure^L. Exposure^R's scale run 2-0, where 0 indicates complete range loss, 1, range stability and 1>2 range expansion.

To explore the impact of future exposure under the SRES A1B scenario, and any variation that might be apparent between Orders and realms the entire LHTd (n=1084) dataset was utilised. Table 4.2 illustrates the division of species between the Orders represented in the LHTd.

Order	**Records (N)**	**Order**	**Records (N)**
Artiodactyla	38	Macroscelidea	9
Carnivora	82	Microbiotheria	1
Chiroptera	294	Peramelemorphia	1
Cingulata	3	Perissodactyla	5
Dasyuromorphia	1	Pholidota	1
Dermoptera	1	Pilosa	7
Didelphidae	24	Primates	26
Diprotodontia	5	Rodentia	499
Eulipotyphla	65	Scandentia	2
Hyracoidea	1	Sirenia	1
Lagomorpha	18		

Table 4.2 Number of Species represented in each Orders across the LHTd.

Future exposure values range between total loss, where the percentage current distribution remaining at 2080 is predicted to be zero, to a species which is predicted to undergo an extreme expansion in distribution, expanding by 475% the area over which it currently resides (Figure 4.3). The mean value of Future Exposure^{R} is 80% of current at 2080, meaning that on average species are predicted to lose around 20% of their current distribution by 2080. There are two species which are predicted to lose their entire range under future exposure; two Rodentia, the Desert pygmy mouse (*Mus indutus*) and the Pale Gerbil *(Gerbillus perpadillus*) which is endemic to Egypt. There is one species for which expansion is classified as extreme in SPSS, this is statistically determined as values 3 times above the interquartile range of the data. The species is the Smoke-bellied rat (*Niviventer eha*), a member of the order Rodentia found in East and Southern Asia, predicted to expand its current distribution by 4.75 times. Figure 4.3, a boxplot shows the range of Exposure$^{R.}$ each Order is predicted to experience and explores in more detail the impact of Future Exposure across the Orders in the LHTd. Using GLM to analyse the influence of Order on Exposure^{R} the Order to which a species belonged was found to have virtually no influence in determining Exposure^{R} (F (20,1063)=1.904, *p*=.01, η^2=0.035). There are 8 species classed as outliers by SPSS, these are values identified as 1.5 times outside the data's interquartile range. These include 2 Chiroptera (Greater sack-winged bat (*Saccopteryx bilineata*) and Miller's long-tongued bat (*Glossophaga longirostris*)), 3 Eulipotyphla (African pygmy hedgehog (*Atelerix albiventris*), Fraser's musk shrew (*Crocidura poenis*) and Large-eared grey shrew (*Notiosorex evotis*)) and 4 Rodentia (Sonoran woodrat (*Neotoma* phenax), Florida mouse (*Podomys floridanus*) and the Sinaloan pocket mouse (*Chaetodipus permix*)). These species experience growth in distribution expanding between 85% (*Atelerix albiventris*) and 140% (*Chaetodipus premix*) on top of their current range size by 2080 under the SRES A1B scenario.

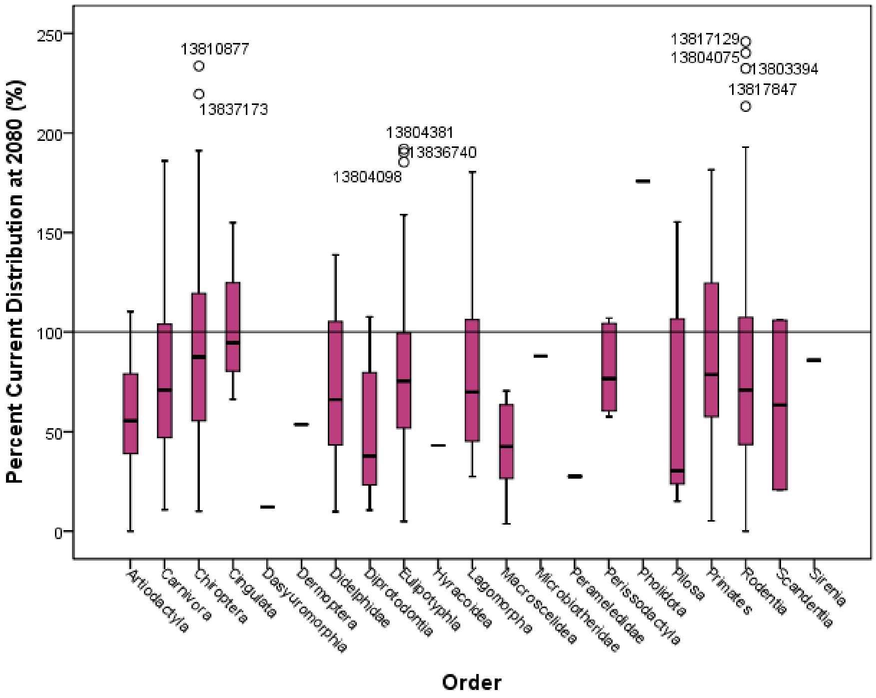


Figure 4.3 Boxplots of Future Exposure by Order (Percentage Current Distribution at 2080) The line at 100% indicates that the distribution size remains stable, below which distribution constricts and above which expansion is predicted to occur. Outliers are indicated by species ID number

The majority of Orders are expected to experience contraction in current distribution by 2080, with the exception of the Pholidota (Pangolin and Scaly Anteaters) with a mean expansion of 75.6% above current distribution (n=1, mean Exposure^{R} =175.6%)(Table 4.3 Descriptive statistics: Exposure by Order (Minimum Exposure refers to greatest contraction and Maximum to smallest contraction in current distribution size to 2080). Species with fewer than five records (highlighted in grey) are omitted from further analysis.Table 4.3). When discounting Orders for which there are fewer than 5 species, the average species Exposure^{R} (percent range remaining at 2080) across the Orders is between 88.3% (Chiroptera, n=294) and 42.8% (Macroscelididae, n=9). The only other Order to have a mean Exposure^{R} value within the quartile of representing the most Exposed (Mean Exposure^{R} <71.5%) are the Artiodactyla (n=38, Mean Exposure^{R} =58.2%). The Orders within the quartile representing least Exposed (Mean Exposure^{R} =>79.8%) the Chiroptera (n=294, Mean Exposure^{R} =88.3%), the Primates (n=26, Mean Exposure^{R}=86.3%) and the Lagomorpha (n=18, Mean Exposure^{R} =80.1).

Descriptive Statistics

Order	Species (N)	Exposure^R (% range remaining at 2080) Maximum	Minimum	Mean	Standard Deviation
Artiodactyla	38	110	0	58.2	29.0
Carnivora	82	186	11	76.6	39.4
Chiroptera	294	234	10	88.3	44.3
Cingulata	3	155	66	105.3	45.4
Dasyuromorphia	1	12	12	12.2	
Dermoptera	1	54	54	53.6	
Didelphimorphia	24	139	10	71.5	40.3
Diprotodontia	5	108	24	51.8	40.7
Eulipotyphla	65	192	5	78.0	42.7
Hyracoidea	1	43	43	43.1	
Lagomorpha	18	180	27	80.1	41.8
Macroscelidea	9	70	4	42.9	23.7
Microbiotheria	1	88	88	88.0	
Peramelemorphia	1	28	28	27.5	
Perissodactyla	5	107	58	81.2	23.5
Pholidota	1	176	176	175.6	
Pilosa	7	155	15	66.0	61.8
Primates	26	181	5	86.3	50.9
Rodentia	499	575	0	78.9	50.2
Scandentia	2	106	21	63.3	60.0
Sirenia	1	86	86	86.0	

Table 4.3 Descriptive statistics: Exposure by Order (Minimum Exposure refers to greatest contraction and Maximum to smallest contraction in current distribution size to 2080). Species with fewer than five records (highlighted in grey) are omitted from further analysis.

The family expected to experience the most Exposure to climate change, excluding those families with fewer than 5 records, is the Macroscelidea (Elephant Shrews) family Macroscelididae (n=9, Exposure^R =42.88%) with an average loss of 57.12% of their current distribution size by 2080. The family predicted to be least impacted are the

Nycteridae (n=6, Exposure^R =141.25%), members of the Chiroptera, with an average expansion of 41.25%.

Future Exposure of Tropical versus Temperate Species

To investigate whether there is variation in Exposure due to biogeographic realm, a boxplot of exposure by biogeographic realm was created (Figure 4.4).

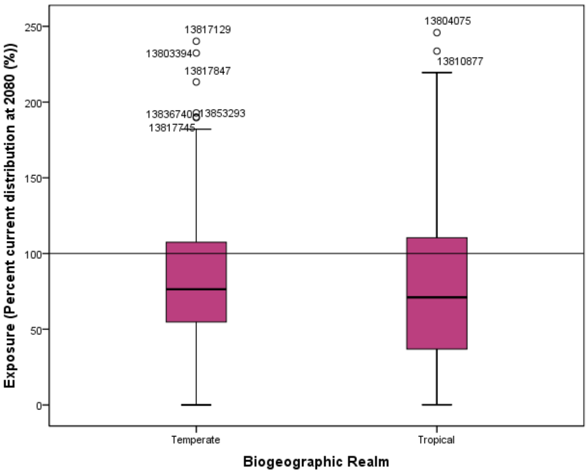


Figure 4.4 Future Exposure^R by Biogeographic Realm (% range remaining at 2080)

There is little visible variation in Exposure^R values across the biogeographic realms, although the range of Exposure^R in the tropical zone appears wider than that of the Temperate zone. Thus, to discover whether there is any significant differentiation in Future Exposure^R between tropical and temperate species a univariate GLM was run across the entire LHTd (n=1084). There are 434 Temperate species and 645 Tropical species represented in the full LHTd. Variation in Future Exposure^R values could not be attributed to whether the species is tropical or temperate (F (1,1077)=1.689, p=0.194, η^2=0.002).

Nine of the Twenty-one Orders represented in the full LHTd have species represented in both Tropical and Temperate realms. In running a GLM across the realms by Order there was only one Order which showed a significant difference in Future Exposure^R determined by realm, the Rodentia (F(1,495)=4.99, p=0.02)(Table 4.4). The

Macroscelidea are the only Order for which the realm to which a species belonged had any influence on the likely Exposure^R (F (1,7)=1.65, *p*=0.24, η^2=0.19), however, the test is non-significant meaning that this conclusion is unlikely to be robust.

Order	**Source**	**Degrees of Freedom**	**F**	**Significance *(P)***	**Eta Squared (η^{2})**
Artiodactyla	Realm	1	0.19	0.66	0.006
	Error	34			
Carnivora	Realm	1	0.04	0.84	0.001
	Error	79			
Chiroptera	Realm	1	0.01		
	Error	292		0.89	0
Didelmorphia	Realm	1	2.22	0.15	0.092
	Error	22			
Eulipotyphla	Realm	1	0.90	0.76	0.001
	Error	63			
Lagomorpha	Realm	1	1.58	0.22	0.09
	Error	16			
Macroscelidea	Realm	1	1.65	0.24	0.191
	Error	7			
Rodentia	Realm	1	4.99	0.02	0.01
	Error	495			

Table 4.4 Results of a GLM describing the Influence of Biogeographic realm on Species Exposure^R by Order

Variation in Exposure across Biogeographic Zones

To investigate whether the degree to which future exposure is likely to impact species differently across the major biogeographic zones a series of further tests were undertaken with the LHTd split by biogeographic zones. The Nearctic zone has the lowest average loss of distribution at 9.7% (Mean Exposure^R =90.3%) and the Palearctic zone the greatest mean loss at 36.1% (Mean Exposure^R =63.9%)(Table 4.5). The

Palearctic zone (species n=108) also has the narrowest range of Exposure^R values around the mean.

Biogeographic Zone	**Species** (N)	**Maximum Exposure^R** (Percent range remaining at 2080)	**Minimum Exposure^R** (Percent range remaining at 2080)	**Mean Exposure^R** (Percent range remaining at 2080)	**Standard Deviation**
Neotropical	321	5	246	78.5	44.9
Australia	27	11	147	81.5	39.7
Afrotropical	247	0	192	77.0	52.5
Oriental	50	4	575	80.9	80.9
Saharo-Arabian	33	0	139	71.8	30.4
Nearctic	293	4	240	90.3	42
Palearctic	108	0	151	63.9	24.3
Total	**1084**	**0**	**575**	**80.0**	**47.7**

Table 4.5 Descriptive Statistics of the LHTd split by biogeographic zone: where maximum exposure describes the greatest percentage contraction of distribution and minimum the smallest percentage contraction.

The distribution of Future Exposure^R values across biogeographic zones is not the same across all zones (Independent Kruskal-Wallis test *p*=0.00). The performance of a ANCOVA to investigate whether Future Exposure^R is linked to biogeographic zone, whilst controlling for Order, determined that the biogeographic zone to which a species belongs is significant in determining future exposure (F (7,1071)=5.073, *p*=0.00, η^2=0.02). However, the effect size of biogeographic zones in determining exposure is weak (η^2=0.02). Figure 4.5, comprises a boxplot of Exposure^R by Biogeographic zone, illustrates variation in Exposure^R.

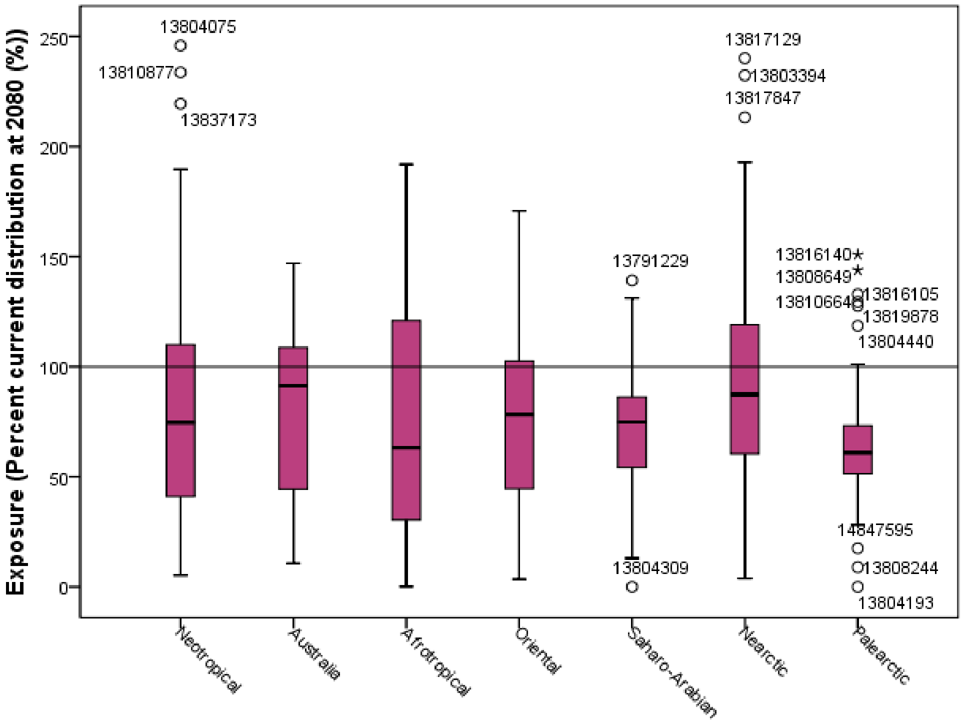


Figure 4.5 Boxplots of Exposure across Biogeographic Zones (% current distribution at 2080) The line at 100% indicates that the distribution size remains stable, below which distribution constricts and above which expansion is predicted to occur. Outliers are indicated by species ID number

The Afrotropical zone has the greatest percentage of species classified as being Most Exposed, with less than 45% of their current range remaining by 2080 (n=128(247), 39.9%). The next 'most exposed' region is the Neotropical zone (n=86(321), 26.8%), followed by the Oriental zone (n=13(43), 26%).

In an investigation of the impact of Exposure^{R} across zones upon individual orders using GLM (Table 4.6), the Artiodactyla were the only Order in which biogeographic zone significantly explained variation in exposure, with a moderate effect (F (3,32)=5.85, p=0.00, η^2=0.35). Biogeographic zone was also found to modestly influence future Exposure^{R} for the Macroscelidea (Elephant Shrews), although this result was non- significant (F (3, 14) =1.65, p=0.24, η^2=0.19). Significant results were also found for the Rodentia (p=0.00, $\eta^{2=}$0.03) and the Chiroptera (p=0.01, η^2=0.05), although the degree to which biogeographic zones influence variation in Exposure^{R} values was negligible.

Order	Source	Degrees of Freedom	F	Significance *(P)*	Eta Squared (η^{2})
Artiodactyla	Zone	3	5.85	0.00	0.35
	Error	32			
Carnivora	Zone	5		0.51	0.05
	Error	75	0.86		
Chiroptera	Zone	6	2.58	0.01	0.05
	Error	294			
Didelmorphia	Zone	1	2.22	0.15	0.09
	Error	22			
Eulipotyphla	Zone	4	0.723	0.57	0.04
	Error	60			
Lagomorpha	Zone	3	1.99	0.16	0.3
	Error	14			
Macroscelidea	Zone	1	1.65	0.24	0.19
	Error	7			
Primates	Zone	2	0.132	0.87	0.01
	Error	23			
Rodentia	Zone	6	3.23	0.00	0.03
	Error	490			

Table 4.6 Results of GLMs testing Exposure^{R} across Biogeographic Zones by Major Orders

4.3.2 Future Exposure within the LHTd 213

Across the set of 213 LHTd records future Exposure^{R} values ranged between 5% (Exposure^{R} =0.05) of suitable habitat remaining at 2080 to an almost doubling of a species range to 190% (Exposure^{R} =1.90), with an average loss of 19% of the species current distribution (Exposure^{R} =0.81). The Order to which a species belongs has a significant weak association (F (14,194) =1.686, *p*=0.06, η^{2}=0.10) with to the degree of Exposure^{R} the species is predicted to experience. Figure 4.6explores the differences across the Orders in terms of future Exposure^{R}.

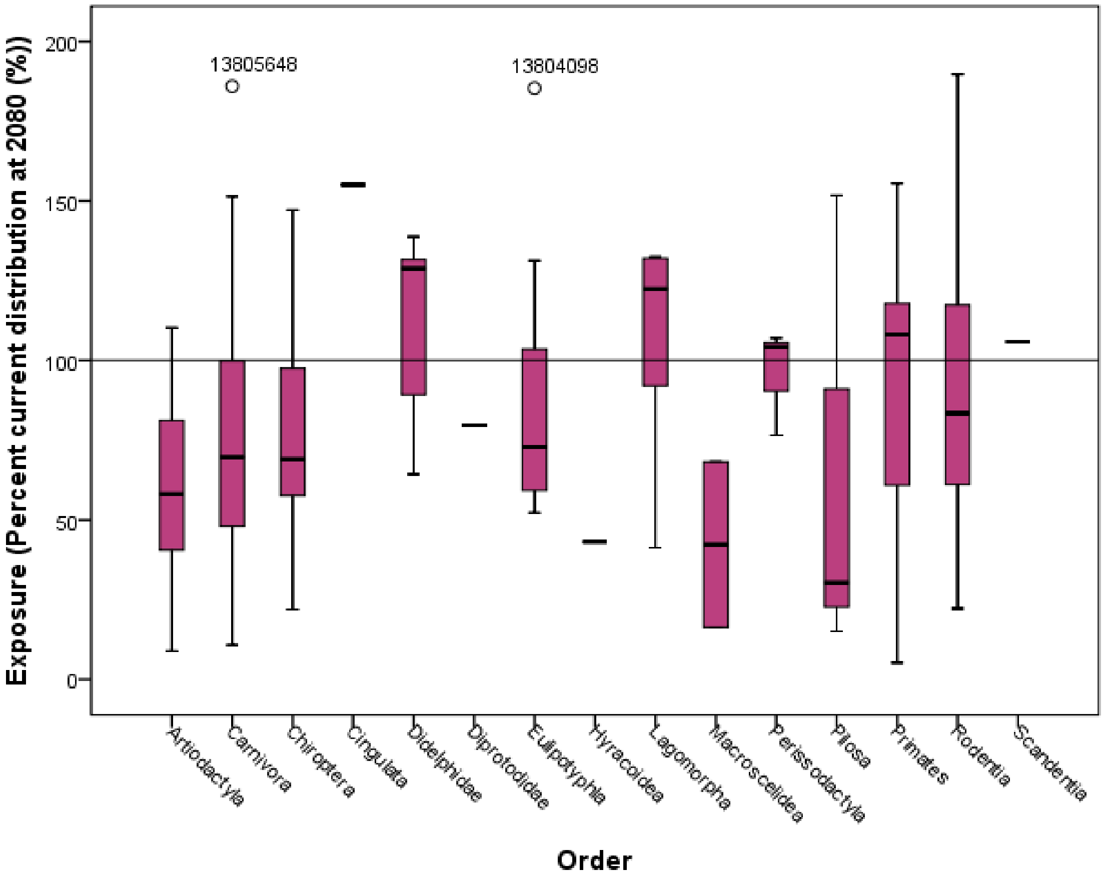


Figure 4.6 Boxplots of Future Exposure^R by Order for the LHTd213 (Percent current distribution at 2080). The line at 100% indicates that the distribution size remains stable, below which distribution constricts and above which expansion is predicted to occur. Outliers are indicated by species ID number.

The Order with the greatest average Exposure is the Artiodactyla with an average percent reduction in range to 62.56% of current distribution across the 21 species represented. The Didelmorphia, the Opossums, are the group which experience the least Exposure to climate change with their distributions staying fairly stable with an average predicted expansion of 10% above current range (Mean Exposure^R =1.10).

The Dusky titi (*Callicebus moloch*), a species of monkey endemic to Brazil, is most at risk, losing 95% of its current distribution extent by 2080 (Exposure^R =0.05). The species with the largest predicted future expansion is the Red-tailed ground squirrel (*Spermophilus tertricaudus*) a species of the family Sciuridae (Squirrels), it is predicted to almost double its current range (Exposure^R =1.90). The two outlying records represent the Carnivora species, the Common kusimanse (*Crossarchus obscurus,* Exposure^R =1.86) a species of dwarf mongoose and the Eulipotyphla species, the African pygmy hedgehog (*Atelerix albiventris*, Exposure^R =1.85). The Muridae (the mice) family of the Rodentia have the smallest degree of standard deviation around the mean at SD =15.4%, whilst the Carnivora family the Herpestidae (the Mongooses) have the largest at SD=63.7%

There are 67 species predicted to expand their range by 2080 under the business-as-usual scenario 32% of the total species; of these 9 are predicted to expand their ranges by upwards of 50% above their current range. There are 16 species predicted to expand their ranges by up to 10%, 42 species are predicted to expand by between 10>50 %.

Future Exposure of Tropical versus Temperate Species

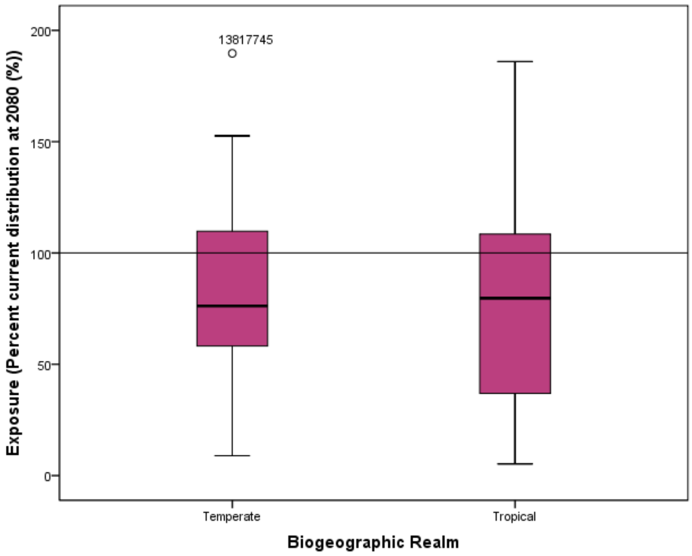
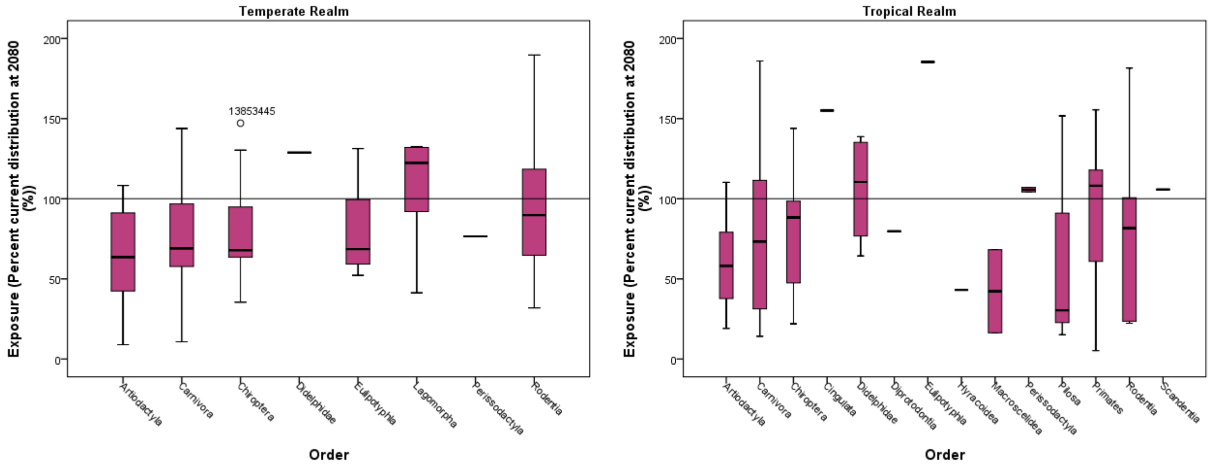


Figure 4.7 Future Exposure^R by Biogeographic Realm for the LHTd213 (Percent current distribution at 2080). The line at 100% indicates that the distribution size remains stable, below which distribution constricts and above which expansion is predicted to occur. Outliers are indicated by species ID number.

Figure 4.7, compares Exposure across the two biogeographic realms, this figure is directly comparable with Figure 4.5 featured in section 4.3.1. The boxplots in Figure 4.8 represent the range of Future Exposure^R value across the individual Orders within the realms. Seven of the Fifteen Orders represented in the LHTd213 have species represented in both Tropical and Temperate realms. In running a GLM across the realms by Order there are two Order which reported a significant difference around the mean between Future Exposure^R determined by realm. The two orders were the Eulipotyphla (F (1, 12) =16.99, p=0.01, η^2=0.58) and Chiroptera (F (1, 22) =0.125, p=0.00, η^2=0.06). The Eulipotyphla and the Didelphidae are the two Orders for which the realm to which a species belonged had any influence on the likely Exposure. The strongest impact of realm was found for the Eulipotyphla (Hedgehogs, Shrews and True Moles) where it had a strong effect (F (1, 12) =16.99, p=0.00, η^2=0.58). A weak effect is recorded for the Didelmorphia (American Possums) (F (1, 3) =0.333, p=0.604, η^2=0.10), although the result is non-significant.



a) **b)**

Figure 4.8 Major Orders split by Biogeographic realm, a) Temperate b) Tropical (The line at 100% indicates that the distribution size remains stable, below which distribution constricts and above which expansion is predicted to occur. Outliers are indicated by species ID number.

Future Exposure by Biogeographic Zone

To investigate whether the degree to which Future exposure is likely to impact species differently across the major biogeographic zones a series of further tests were undertaken with the LHTd213 split by biogeographic zones. The Nearctic zone has the lowest Mean Exposure^R at 98.5% of current distribution at 2080 (n=76) (n=2). The Palearctic zone is the zone in which the greatest mean loss occurs, with an average loss of 42.2% (n=43, Mean Exposure^R =57.8%) (Table 4.7). These results are similar to those determined using the full data set (Section 4.3.1) with variation in mean Exposure^R between the two sets of 8.2% for the Nearctic zone and 6.1% in the Palearctic zone.

Biogeographic Zone	**Species** (N)	**Maximum Exposure^{R}** (% current distribution at 2080)	**Minimum Exposure ^{R}** (% current distribution at 2080)	**Mean Exposure^{R}** (% current distribution at 2080)	**Standard Deviation** (SD %)
Neotropical	34	5	182	91.8	46.4
Australia	2	80	94	86.9	10.2
Afrotropical	37	14	186	67.9	47.5
Oriental	11	22	144	79.9	38
Saharo-Arabian	6	28	104	65.6	25.7
Nearctic	76	32	190	98.5	31.1
Palearctic	43	9	97	57.8	16.6
Total	**209**	**5**	**190**	**81.6**	**38.8**

Table 4.7 Descriptive statistics of Exposure^{R} values across the Biogeographic zones for the LHTd213

The distribution of Future Exposure^{R} values across biogeographic zones is not the same across all zones (Independent Kruskal-Wallis test p=0.00). The performance of an ANCOVA to investigate whether Future Exposure^{R} was linked to biogeographic zone, whilst controlling for Order, suggests that biogeographic zone did have a significant modest influence over future Exposure^{R} (F (6,202)=7.7, p=0.00, η^2=0.19).

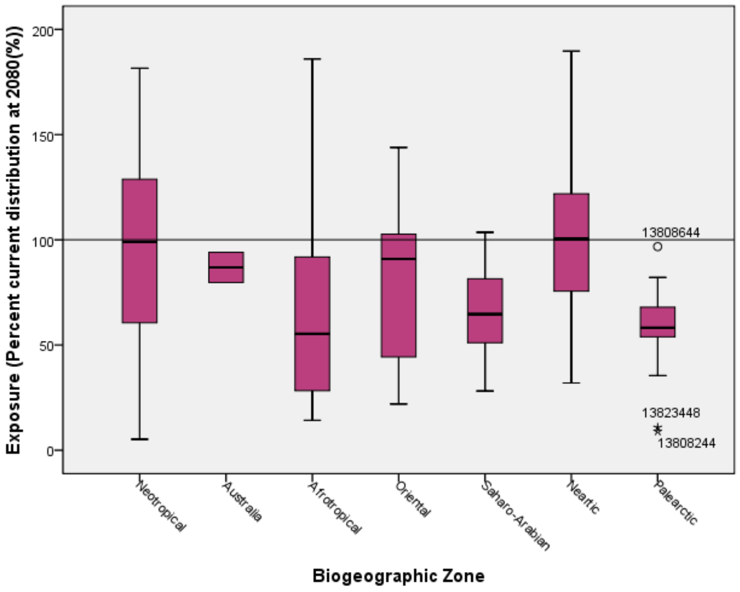


Figure 4.9 Future Exposure^{R} by Biogeographic Zone Boxplot for the LHTd213 (The line at 100% indicates that the distribution size remains stable, below which distribution constricts and above which expansion is predicted to occur. Outliers are indicated by species ID number.)

Figure 4.9 illustrates the variation in Exposure^R across the biogeographic zones. The suite of species occurring within the Palearctic (n=43) and Australian (n=2) zones experience a degree of contraction in distribution from current to 2080. Species represented in the Afrotropical (n=37) and Saharo-Arabian (n=6) are also predominantly expected to experience contraction.

A GLM was undertaken to investigate whether Exposure^R impacted individual orders differently dependent on zones(Table 4.8). Only those Orders spanning more than a single zone were included in the test. Variation in Exposure^R across the biogeographic zones was significant for the orders Eulipotyphla and Rodentia. Biogeographic zone was found to strongly influence the degree to which individual species of the Eulipotyphla were predicted to be exposed in the future (F (3, 14) =26.4, *p*=0.00, η^2=0.88), and modestly influence the Rodentia (F (5, 53) =3.15, *p*=0.01, η^2=0.22). Biogeographic zone moderately influenced Exposure^R for both the Chiroptera (F (5, 18) =2.46, *p*=0.07, η^2=0.40) and Artiodactyla (F (3, 17) =2.68, *p*=0.08, η^2=0.32) although the results were non-significant.

Order	**Source**	**Degrees of Freedom**	**F**	**Significance *(P)***	**Eta Squared (η^{2})**
Artiodactyla	Zone	3	2.68	0.08	0.32
	Error	17			
Carnivora	Zone	5	1.88	0.14	0.15
	Error	52			
Chiroptera	Zone	5	2.46	0.07	0.40
	Error	18			
Eulipotyphla	Zone	3	26.4	0.00	0.88
	Error	14			
Rodentia	Zone	5	3.15	0.01	0.22
	Error	53			

Table 4.8 Results of a GLM across biogeographic zones by Order

4.3.3 Sensitivity by biogeographic zone

An analysis of the distribution of Sensitivity across biogeographic zones, not considered in Chapter Three, using the GLM revealed that Sensitivity varied significantly across the biogeographic zones ($F(6,202)=4.11$, $p=0.00$, $\eta^2=0.11$) exerting a modest influence on sensitivity score. The Neotropical zone had the largest mean Sensitivity (n=34, $S=10.74$) and the Oriental zone the smallest mean Sensitivity (n=11, $S=8.24$), where the Australian zone is excluded due to lack of records (n=2).

Differences amongst Sensitivity values were assessed using ANOVA to compare between groups' variation in Exposure^R across the zones. Difference across the temperate zones Palearctic, Nearctic, and Saharo-Arabian were non-significant (Palearctic vs. Nearctic, $n=119$, $p=0.83$, Palearctic vs. Saharo-Arabian, $n=39$, $p=0.76$ and Nearctic vs. Saharo-Arabian, $n=82$ $p=0.98$).

Comparisons between tropical zones, using ANOVA showed non-significant variation between Australia and the Oriental and Afrotropical zones (Australia vs. Oriental, $n=13$, $p=0.430$, Australia vs. Afrotropical, $n=39$, $p=0.065$). Significant variation across sensitivity between tropical zones were recorded for all combinations involving the Neotropical zone (Neotropical vs. Australia, $n=36$, $p=0.038$, $\eta=0.12$, vs. Afrotropical, $n=71$, $p=0.02$, $\eta=0.07$, vs. Oriental, $n=45$, $p=0.01$, $\eta=0.22$). There was also a significant difference recorded between the Afrotropical and Oriental zone ($n=48$, $p=0.01$, $\eta=0.11$).

GLM was used to investigate whether there were significant differences in Sensitivity across biogeographic zones by Order. There are five orders for which there is data available across more than 2 zones, the Artiodactyla, Carnivora, Chiroptera, Eulipotyphla and Rodentia (Table 4.9).

Order	**Source**	**Degrees of Freedom**	**F**	**Significance *(P)***	**Eta Squared (Ƞ^{2})**
Artiodactyla	Zone Error	3 21	1.076	0.38	0.16
Carnivora	Zone Error	5 52	1.309	0.27	0.11
Chiroptera	Zone Error	5 18	2.49	0.06	0.41
Eulipotyphla	Zone Error	2 10	0.568	0.64	0.14
Rodentia	Zone Error	5 53	0.34	0.88	0.03

Table 4.9 GLM results comparing Sensitivity scores acorss zones by Order

There were no Orders for which there was a significant difference in Sensitivity across the zones. However, for the Orders Chiroptera, Artiodactyla, Eulipotyphla and Rodentia the zones did contribute to variation in Sensitivity although all were non-significant (Chiroptera (F(5,18)=2.49, *p*=0.06 Ƞ=0.41, moderate), Artiodactyla (F(3,21)=1.07,*p*=0.38 Ƞ=0.16, modest), Eulipotyphla (F(2,10)=0.56, *p*=0.64 Ƞ=0.14, modest), Carnivora,(F(5,52)=1.30, *p*=0.27 Ƞ=0.11, modest)).

4.3.4 **Future Vulnerability**

To explore the predicted impact of future Climate change Exposure on species, and the Orders to which they belong, a scatterplot was created using Sensitivity values on the y-axis and Exposure^{L} (proportion distribution loss on the x-axis). Exposure^{L} is the value used to calculate Vulnerability and as such is always used when discussing Vulnerability.

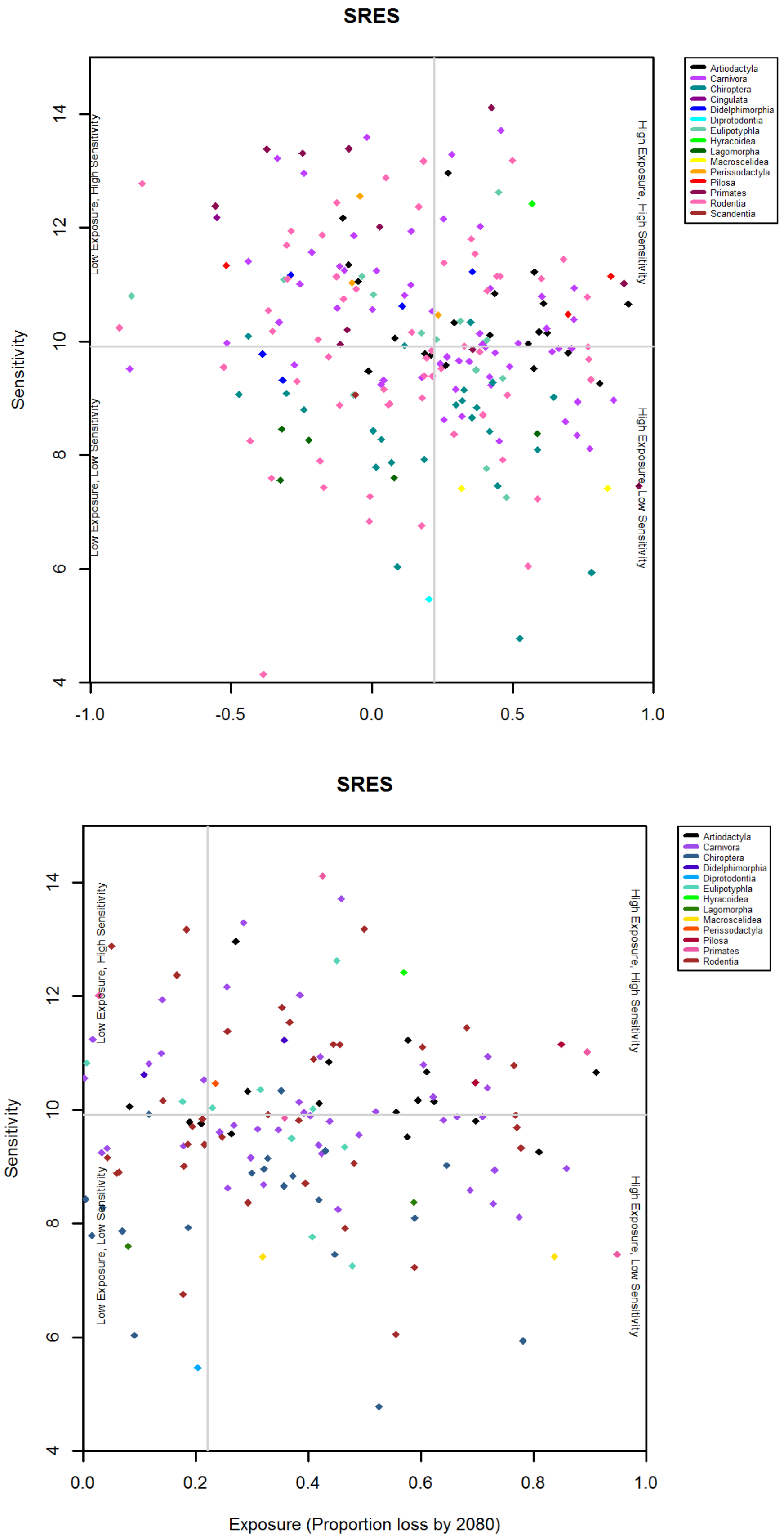


Figure 4.10 Future Vulnerability by Order Scatterplot a) All species b) Species experiencing range contraction

In order to illustrate fully the variation in Future exposure across the species set Figure 4.10(a & b), shows the data with shifted axis. Figure 4.10 shows all species taking into account those species with expanding distributions i.e. exposure above 0 to -1. Figure 4.10b shows the species experiencing contraction in their current distribution, where zero represents a stable distribution and 1 equals total loss

There are 78 species, 37% of the total species, which fall within the Highly Vulnerable classification. A Pearson's product moment correlation coefficient was computed to assess the relationship between Sensitivity and Future Exposure^L. There is a modest, significant correlation between Sensitivity and Future Exposure^L ($r=0.164$, $n=209$, $p=0.01$), hence there is also a small relationship between a species sensitivity and predicted change in its distribution due to climate change. To test whether there is an association between Sensitivity and Future Exposure^L scores and the Order to which a species belong a univariate GLM was carried out. Variation within Sensitivity values was modestly linked with the Order to which the species belongs, explaining 29% of the between-subjects variation ($F(1, 14) = 5.542$, $p=.000$, $\eta^2=0.29$). However, variation in the degree to which a species is predicted to be exposed to future climate change appears more complex, and is only weakly correlated with the Order to which it belongs ($F(1, 14) = 1.68$, $p=0.06$, $\eta^2= 0.10$). The Orders to which a species belongs is a significant factor in explaining individual species Vulnerability explaining 16% of the variation, considered to be a modest effect ($F(1, 14) = 2.55$, $p= 0.02$, $\eta^2= 0.16$).

The composite Vulnerability score ranges between -0.39 for the least Vulnerable species, the Cotton Mouse (*Peromyscus gossypinus)*, and 1.58 for the most Vulnerable species, the Brown-mantled tamarind (*Saguinus fuscicollis)*. The mean species Vulnerability score is 0.76 with a range between the scores for Extremely Vulnerable to Least Vulnerable of 1.96. The degree to which a species is described as Vulnerable is assessed on the basis of the range of the Vulnerability within the data. As previously described those species within the upper quartile (U.Q. =0.89) are most Vulnerable, and those below the lower quartile (L.Q. =0.40) are least Vulnerable. There are 78 species in the Most Vulnerable and 39 species in the Least Vulnerable classifications as determined by the quartiles in the data. The top 10% of Most Vulnerable species (n=12) include, four Rodentia, three Carnivora, 2 Primates, 1 Artiodactyla, 1 Pilosa and the

Hyrax. Within this top 10% there are eight species classified as Extremely Vulnerable, with Vulnerability scores above 1.4.

Future Vulnerability Within Orders

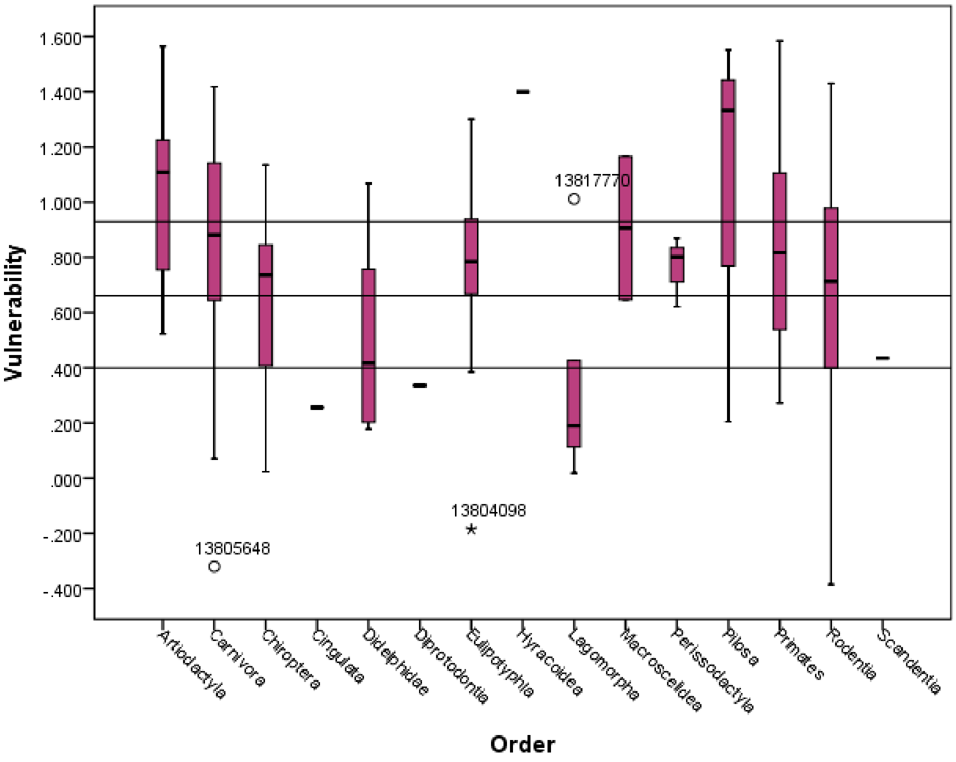


Figure 4.11 Boxplot representing Vulnerability Score by Order

In examining Vulnerability scores across Orders (Figure 4.11, Table 4.10), the Artiodactyla (Even-toed ungulates) have the highest mean Vulnerability (n=21, *Vu*=1.00), when removing those Orders with fewer than 5 records. The Order with the lowest mean Vulnerability is the Lagomorpha (n=5, *Vu*=-0.35). The Rodentia have the largest range of Vulnerability values, ranging between –0.385 to 1.43 (n=59, Vulnerability range=1.82). The two outliers with extreme negative Vulnerability values are the Carnivora, the Common kusimanse (*Crossarchus obscurus*, Vulnerability=-0.321), Eulipotyphla, the African pygmy hedgehog (*Atelerix albiventris*, Vulnerability=-0.186). The single outlier with an extreme positive Vulnerability score is the Lagomorpha, the Pika *(Ochtona princeps*, Vulnerability=1.012).

Vulnerability Descriptive Statistics

Order	N	Range	Minimum	Maximum	Mean	Std. Deviation
Artiodactyla	21	1.04	0.523	1.564	1.004	0.286
Carnivora	57	1.73	-0.321	1.418	0.860	0.349
Chiroptera	24	1.11	0.022	1.134	0.629	0.308
Cingulata	1		0.256	0.256	0.256	
Didelphimorphia	5	0.88	0.178	1.067	0.524	0.382
Diprotodontia	1		0.336	0.336	0.336	
Eulipotyphla	14	1.48	-0.186	1.3	0.732	0.352
Hyracoidea	1		1.399	1.399	1.399	
Lagomorpha	5	0.99	0.018	1.012	0.351	0.399
Macroscelidea	2	0.52	0.647	1.165	0.905	0.366
Perissodactyla	3	0.24	0.62	0.869	0.764	0.129
Pilosa	3	1.34	0.205	1.552	1.029	0.723
Primates	11	1.31	0.271	1.585	0.852	0.421
Rodentia	59	1.82	-0.385	1.43	0.676	0.431
Scandentia	1		0.435	0.435	0.435	

Table 4.10 Descriptive Statistics for Vulnerability across the Orders

To assess the degree to which the different Orders are Vulnerable the species of the major Orders were classified as Most Vulnerable to Least Vulnerable using the upper and lower quartile values respectively (Table 4.11).

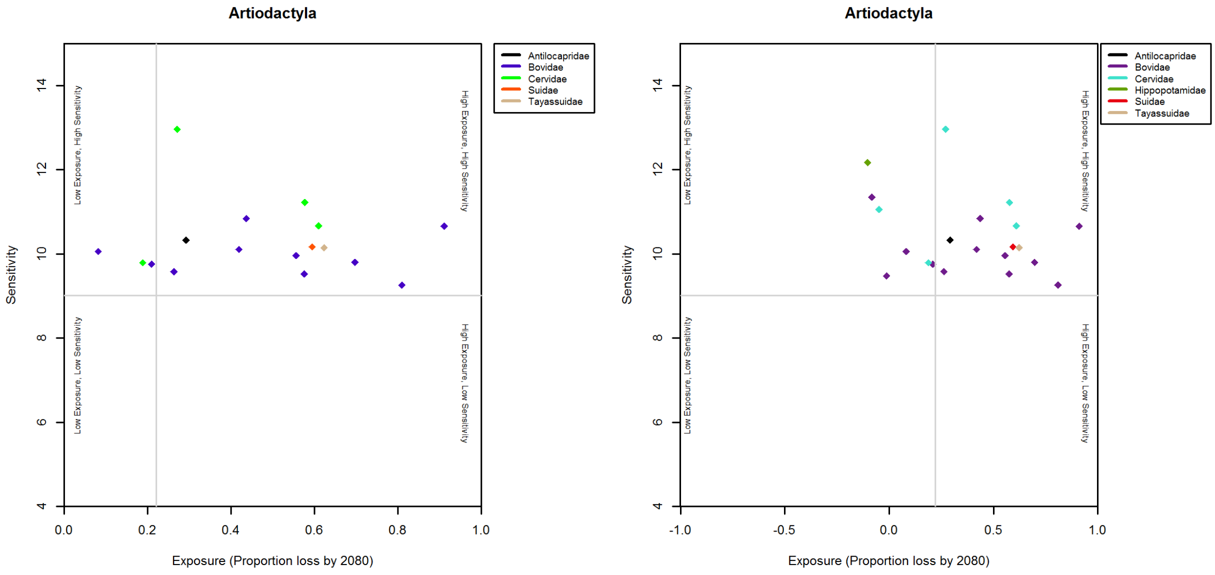
	Most Vulnerable		**Moderately Vulnerable**		**Least Vulnerable**	
Order	**Frequency** (n)	**Percentage** (%)	**Frequency** (n)	**Percentage** (%)	**Frequency** (n)	**Percentage** (%)
Artiodactyla	13	61.9	8	38.1	0	0
Carnivora	27	48.2	24	42.9	5	8.9
Chiroptera	4	16.7	14	58.3	6	25
Didelmorphia	1	20	2	40	2	40
Eulipotyphla	5	35.7	7	50	2	14.3
Lagomorpha	1	20	1	20	3	60
Primates	4	36.4	6	54.5	1	9.1
Rodentia	19	32.2	23	39	17	28.8
Total	74	37.9	85	43.6	36	18.5

Table 4.11 Vulnerability Classifications

The Order with the largest number of species classified as among the Most Vulnerable are the Artiodactyla (61.9%, n=13). The Carnivora are also have a large number of species classified as Most Vulnerable (n=27, 48.2%). The Chiroptera have the fewest species classified as among the Most Vulnerable (16.7%, n=4). The Lagomorpha have the largest percentage of species classified as among the Least Vulnerable (60%, n=3). The Artiodactyla are the sole Order in which no species is classified as being among the Least Vulnerable.

To tease out variation in the contributing factors of Vulnerability within each Order and to explore the combination of both sensitivity and future exposure values in conferring Vulnerability across the Orders scatterplots were created for each of the major orders (i.e. those with 5 or more records).

Artiodactyla

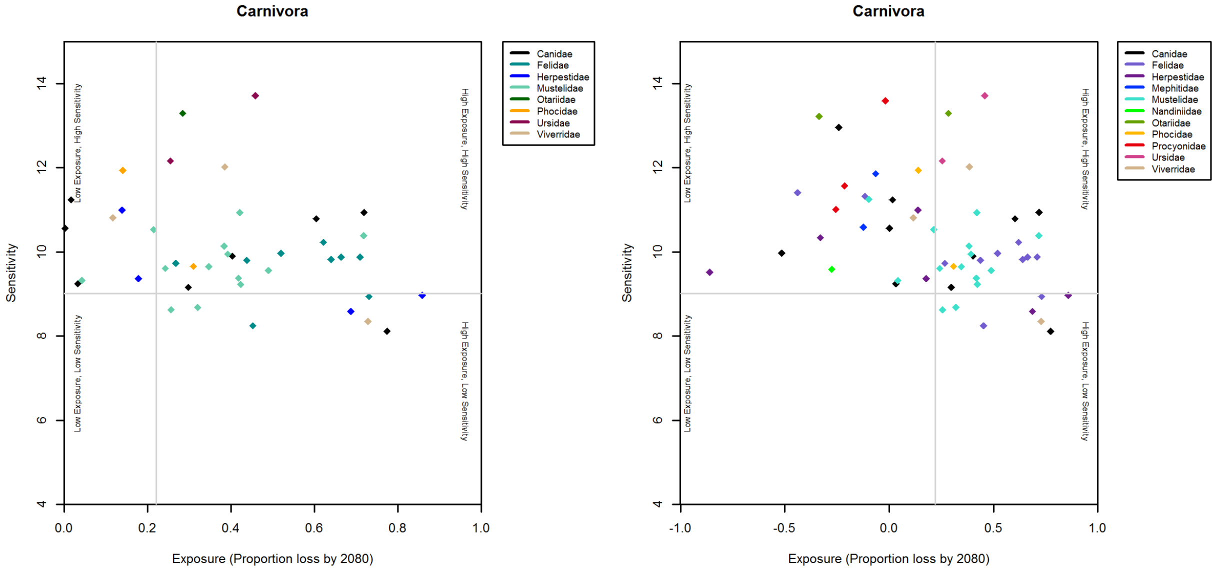


a) **b)**

Figure 4.12 Scatterplots of Future Vulnerability across the Artiodactyla Families, a) Species losing range b) All species

The Artiodactyla have 21 members represented in the LHTd213, 14 are Highly Vulnerable, one of which is classified as Extremely Vulnerable (Figure 4.13a). Each of these Highly Vulnerable species are predicted to lose over 25% of their current range, and are not likely to be able to rapidly adapt to future conditions, indicated by their high Sensitivity scores (above 9.91). The European Bison (*Bison bonasus*) is the most vulnerable Artiodactyla, with a Sensitivity score of 10.66 and predicted to lose 91% of its current distribution by 2080 it has a combined Vulnerability score of 1.56. There are four species projected to expand their ranges although none are expected to expand by above 10% of their current distribution, expansion below which value is considered to be within the natural variation of a species range (Figure 4.13b).

Carnivora

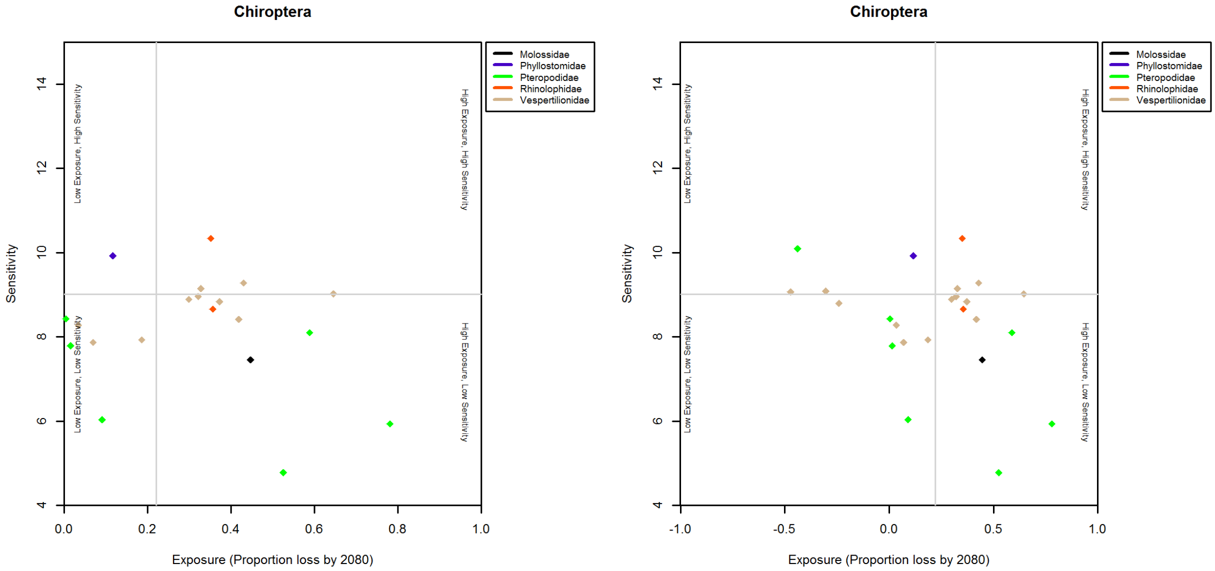


a) b)

Figure 4.13 Scatterplot of Future Vulnerability scores by Family for the Carnivora a) Species losing range b) All species

There are 25 of the 56 Carnivora species which are classified as Highly Vulnerable (Figure 4.14a). This is the category which encompasses the largest number of Carnivora species. The single Carnivora species classified as Extremely Vulnerable is the Brown bear (*Ursus arctos,* Vulnerability=1.41). Seven of the eleven Felidae (Cats) represented in the LHTd are classified as Highly Vulnerable including the Lion (*Panthera leo*, Vulnerability=1.28), Jaguar (*Panthera onca*, Vulnerability=1.23), European Lynx (*Lynx lynx*, Vulnerability=1.23), the Ocelot (*Leopardus pardalis,* Vulnerability=1.21), Leopard (*Panthera pardus*, Vulnerability=1.20), Cheetah (*Acionyx jubatus*, Vulnerability=1.10) and Canada Lynx (*Lynx Canadensis*, Vulnerability=1.00). Five of the Highly Vulnerable Felidae are native to the tropics, with the exception of the two Lynx species. The Sea Otter and Walrus were removed from further analysis due to their dependency on the sea as part of their habitat, which is not modelled here. There are 14 species which are predicted to expand their ranges under the business-as-usual scenario of climate change, with 11 species expanding beyond 10% of their current range by 2080 (Figure 4.14b). However, none of these species fall into the category of Moderate Vulnerability, and therefore are unlikely to fulfil this degree of expansion due to their Sensitivity traits.

Chiroptera

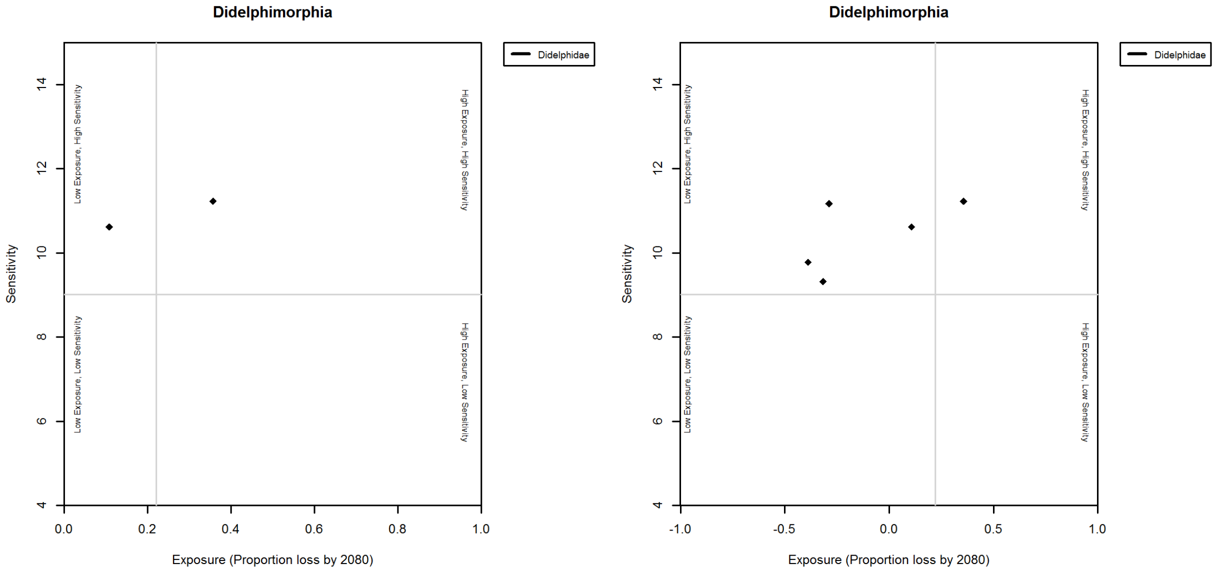


a) b)

Figure 4.14 Scatterplot of Future Vulnerability of Chiroptera species by Family, a) Species losing range b) All species

There are 24 Chiroptera species in the LHTd none of which are classified as Extremely Vulnerable (Figure 4.15a). There are three species classified as being Highly Vulnerable, these are temperate species the Common bent-wing bat (*Miniopterus schreibersii*, Vulnerability=1.134), the Greater Horseshoe bat (Rhinolophus ferrumequinum, Vulnerability=0.97) and the Common Noctule (*Nyctalus noctule,* Vulnerability=0.94) (Figure 1a). The largest group of Chiroptera (n=9) are classified as lowly Vulnerable, being both lowly sensitive and highly Exposed. These species categorised in the Lowly Vulnerable classification are well placed to adapt to future climate change due to their low Sensitivity scores.

Didelphimorphia

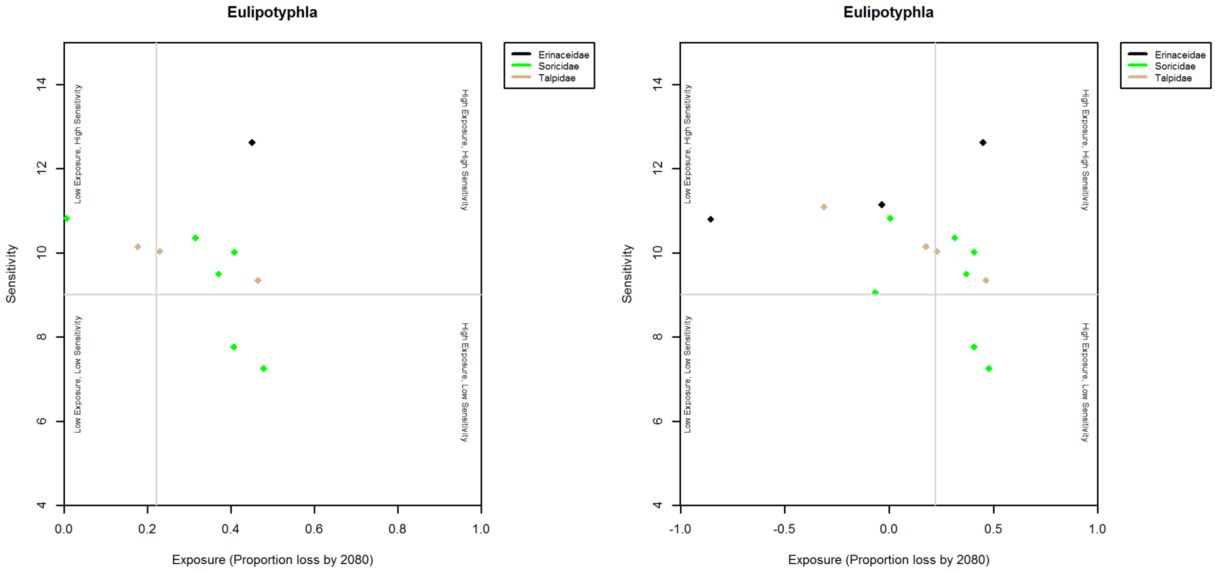


a) b)

Figure 4.15 Future Vulnerability Scatterplot for the Didelmorphia families a) Species losing range b) All species

There are no Didelphimorphia, the Opossums, classified as Extremely Vulnerable by 2080 (Figure 4.16a). The mean Vulnerability score across the Didelphimorphia is 0.52, with a minimum of 0.15 and maximum of 1.06. There is a single species in the Highly Vulnerable category the White-eared opossum (*Didelphis albiventris*, Vulnerability=1.06). The remaining species are classified as Moderately Vulnerable and are at latent risk from climate change, due to their innate Sensitivity. Three of the five species are predicted to expand their ranges (Figure 4.16b), with all three expanding by beyond 10% of their current distribution (Common opossum (*Didelphis marsupalis,* Exposure^{L} =-0.39), Virginia Opossum (*Didelphis virgianus,* Exposure^{L} =-0.29) and Robinson's mouse opossum (*Marmosa robinsoni,* Exposure^{L} =-0.32). Thus, although these species are classified as moderately Vulnerable, due to their Sensitivity these expanding species have low overall Vulnerability scores ranging from 0.17 (*Didelphis marsupalis*) to 0.41 (*Didelphis virgianus*).

Eulipotyphla

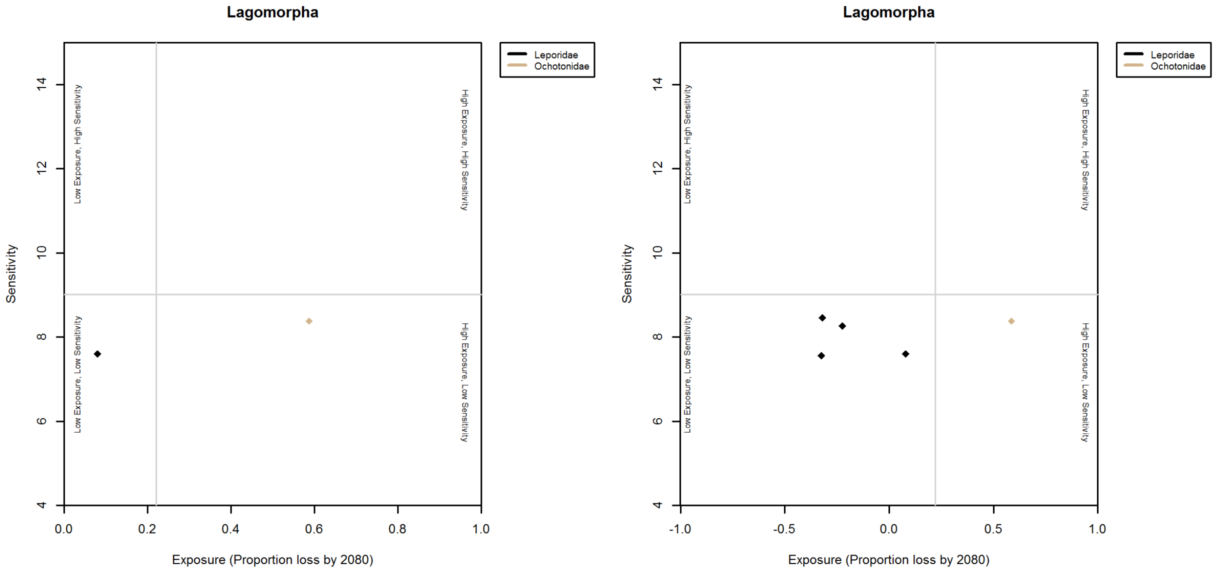


a) b)

Figure 4.16 Future Vulnerability by Family Scatterplot for the Eulipotyphla a) Species losing range b) All species

The Eulipotyphla (n=14), which include the hedgehogs, shrews and moles, have five species categorised as Highly Vulnerable, three Shrews (Soricidae), a Mole (Talpidae) and Hedgehog (Erinaceidae). All of the species fall outside of the 'Extremely exposed' categories with no species projected to lose above 50% of their current range by 2080 (Figure4.16a). The largest group of Eulipotyphla (n=6) are found in the Moderately Vulnerable category on account of their individual Sensitivity scores. However, four of these species are projected to expand their ranges to 2080 lowering their overall Vulnerability. Only two, the African pygmy hedgehog (Exposure^{L} =-0.85) and the Eastern mole (Exposure^{L} =-0.34) are predicted to expand their ranges by over 10% (Figure 4.16b).

Lagomorpha

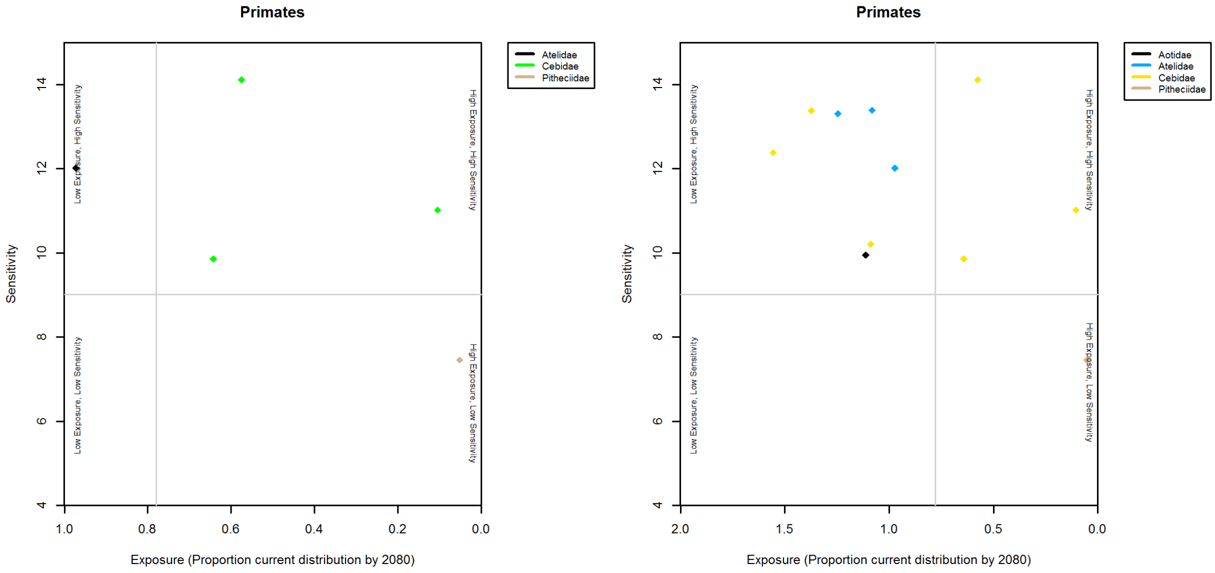


a) b)

Figure 4.17 Future Vulnerability Scatterplot by family for the Lagomorpha a) Species losing range b) All species

There are five species of Lagomorpha represented in the LHTd213 none of which is classified 'Extremely' or 'Highly vulnerable', this is due to the low Sensitivity scores across the species (Figure 4.17a). The four Leporidae (Rabbits) are classified in the Least Concern category, with three of the four species projected to expand their ranges under climate change (Figure 4.17b). The American Pika (*Ochotona princeps*), the sole Pika represented in the LHTd213, is categorised as Lowly Vulnerable, being of least concern, although requiring monitoring.

Primates

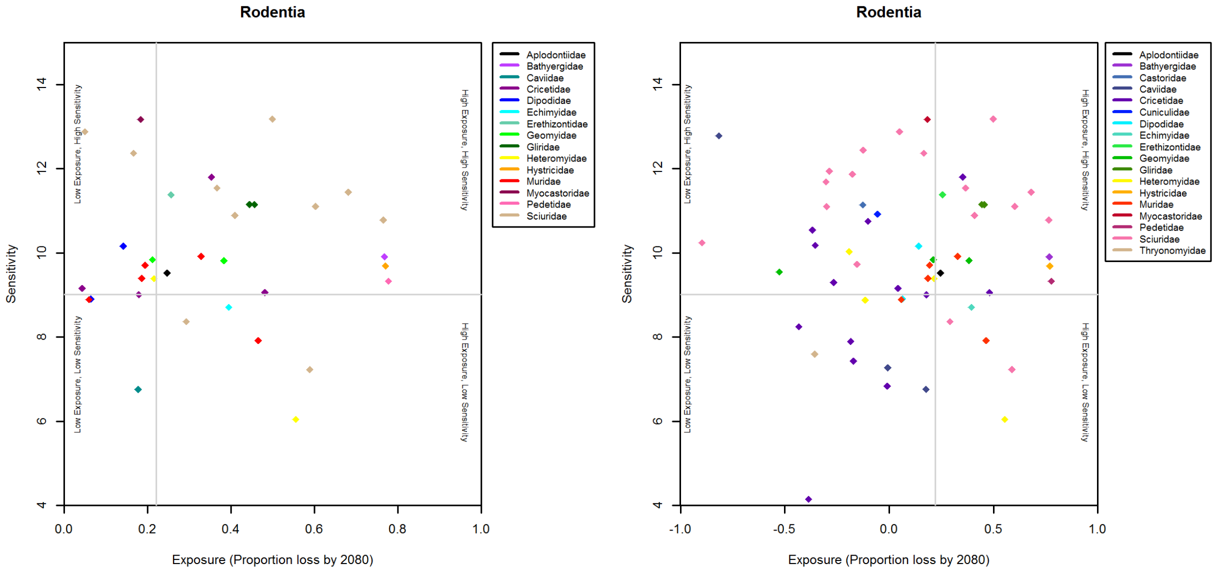


a) b)

Figure 4.18 Future Vulnerability by Family Scatterplot for the Primates a) Species losing range b) All species

There are no Primates categorised as Extremely Vulnerable, however three are classified as 'Highly vulnerable' (Figure 4.18a). Five of the eleven primates represented in the LHTd are predicted to lose part of their distribution, ranging between a contraction of 5% (Geoffroy's spider monkey, *Ateles geoffroyi*) to 95% (Red-bellied titi, *Callicebus moloch*) (Figure 1.18a). The most Vulnerable species is the Brown-mantled tamarind (*Saguinus fuscicollis*, Vulnerability=1.57). The Black-capped capuchin (*Cebus apella*) is the most Sensitive of the Primate species represented (*S*=14.11) although climate change is not predicted to threaten its range (Exposure^{L} =-0.55). Six species are predicted to expand their distributions, with three predicted to expand their ranges above 10% of their current range (Figure 4.18b). However, because each of these has Sensitivity score above 9.5 it is unlikely that these species will realize this expansion into the future.

Rodentia



a) b)

Figure 4.19 Future Vulnerability by Family Scatterplot for the Rodentia, a) Species losing range b) All species

There are 59 species of Rodentia represented in the LHTd213 of which four, all members of the Sciuridae (squirrels) are classified as Extremely Vulnerable (Figure 4.20a). These include the Grey Squirrel (*Sciurus carolinensis*, Vulnerability=1.40), the Red squirrel (*Sciurus vulgaris,* Vulnerability=1.30), the Least Chipmunk (*Tamias minimus* Vulnerability=1.41) and the Cape ground squirrel (*Xerus incuris*, Vulnerability=1.43). Sixteen of the 59, equivalent to 27% of species are classified as Highly Vulnerable with individuals from seven separate families. The largest number of species (n=25) group into the Moderately Vulnerable category, with a further 5 species falling into the lowly Vulnerable category. The 12 species in the Least Concern classification are mainly Cricetidae (n=8), which includes New World rats and mice, true hamsters, voles and lemmings. There are 25 species projected to expand their distributions under future climate change, with 16 of these projected to expand their ranges above 10% (Figure 4.19b).

Future Vulnerability by Biogeographic Realm and across the Zones

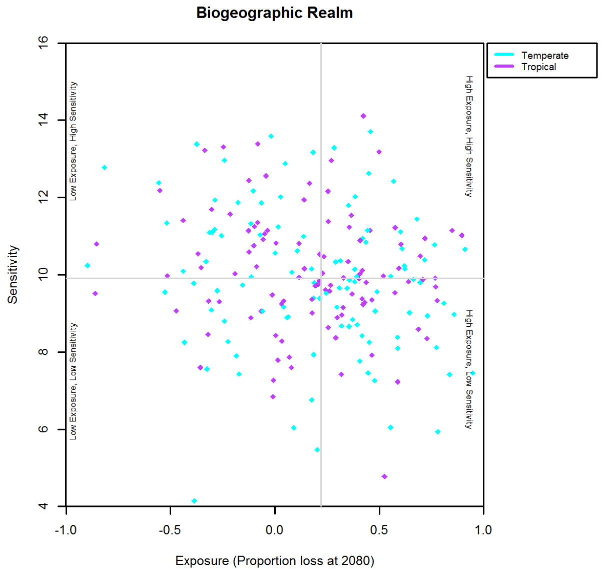


Figure 4.20 Species Vulnerability split by Biogeographic Realm

There are 126 Temperate species and 83 Tropical species represented in LHTd213. Four species were removed from this part of the analysis as their distributions spanned both realms. In the LHTd213 17.4% of Temperate species (n=22) and 27.7% of Tropical species (n=23) are identified as Highly Vulnerable falling into the classification High Exposure^{L}, High Sensitivity (Figure 4.21). The realm to which a species exists, temperate or tropical, has influence on the species Vulnerability score (GLM, F (2,204) =1.66, p=0.27, η^2= 0.00).

The biogeographic zone to which a species belongs has a modest influence on its Vulnerability (ANCOVA, F (7,199) =6.181, p= 0.00, η^2=0.17 (Covariate=Order)).

	Most Vulnerable		Moderately Vulnerable		Least Vulnerable	
Zone	**Frequency**	**Percentage**	**Frequency**	**Percentage**	**Frequency**	**Percentage**
Afrotropical	20	54.1	11	29.7	6	16.2
Australian	0	0	1	50	1	50
Nearctic	18	23.7	36	47.4	22	28.9
Neotropical	10	29.4	17	50	7	20.6
Oriental	3	27.3	5	45.4	3	27.3
Palearctic	25	61	16	39	0	0
Saharo-arabian	2	33.3	4	66.7	0	0
Total	78	37.7	90	43.5	39	18.8

Table 4.12 Vulnerability Classifications by Biogeographic zones

To explore how Vulnerability varies across the zones Vulnerability scores were classified Most to Least Vulnerable using the upper and lower quartiles as previously and the species split along the biogeographic zones (Table 4.12). The Palearctic zone holds the greatest percentage of species classified as Most Vulnerable (n=25, 61%). The Afrotropical zone also has over 50% of species represented classified as Vulnerable (n=20, 54.1%). The Nearctic zone has the largest number of species accounted for in the Least Vulnerable classification and the largest percentage (n=22, 28.9%), when discounting the Australian zone due to its few species. The majority of species for the Nearctic (n=36, 47.4%), Oriental (n=5, 45.4%) and Saharo-Arabian (n=4, 66.7%) zones are classified as moderately Vulnerable.

4.3.5 Testing the Vulnerability Measure

To test whether the calculation of the final Vulnerability score remains relatable to its constituent variables in Sensitivity and Exposure^L a Pearson's correlation test was completed, using *r* as the validation coefficient (Stahl 2013) (Table 4.13). The closer *r* is to 1 the better the validity. This check was carried out to ensure no mistakes had been made in the calculation of the Sensitivity measure.

In combination the Exposure^L and Sensitivity measure were found to perfectly predict the Vulnerability measure (r=1.0, p=0.00), indicating that the Vulnerability measure loses no explanatory power in its creation. Sensitivity is significantly positively correlated with the prediction of Vulnerability, (r=0.275, n=209, p=0.000), showing a moderate relationship to Vulnerability. This shows that the Vulnerability calculation remains true to the earlier finding that Vulnerability increases where species are more sensitive. Exposure^L is shown to strongly correlate with Vulnerability, (r=0.903, n=207, *p*=0.000). In agreement with the conclusion that as a species is more Exposed to climate change the species becomes more Vulnerable.

These correlations were further analysed in a comparison with the component variables making up the PCAf, and which determine the Sensitivity measure. The Vulnerability measure maintains the relationships between the Sensitivity variables identified in Chapter Three. For example, both gestation length and time to sexual maturity are related to species sensitivity, increases in both are reflected in increased Sensitivity. This relationship remains apparent when testing the correlation between the composite Vulnerability measure and gestation length and sexual maturity, an increase in either is relatable to increased Vulnerability with both modestly influencing the final Vulnerability measure (Gestation *r*=0.268, *p*=0.00; Sexual Maturity *r*=0.350, *p*=0.00).

Body mass is known to strongly correlate with several life history traits and has been shown to influence where a species lies on the r-K continuum although is not sufficient as the sole determinant (Purvis *et al.* 2000; Bielby *et al.* 2007). Thus, body mass was included in the analysis to examine the strength of correlation with Vulnerability. Body mass was observed to moderately correlate with Vulnerability (r=-0.263, n=209, *p*=0.00).

		Vulnerability		
Traits		**Pearson Correlation**	**Sig. (1-tailed)**	**N**
	Mass (log.g)	0.263	0.00	207
Exposure^L	**Exposure^L (Proportion Loss)**	0.903	0.00	207
Sensitivity	**Sensitivity**	0.275	0.00	207
Sensitivity Variables	**Weaning Age (log. Days)**	0.236	0.00	207
	Litters per Year (log.N)	-0.262	0.00	207
	Sexual Maturity log.(Days)	0.350	0.00	207
	Longevity (log. Months)	0.305	0.00	207
	Gestation (log. Days)	0.268	0.00	207
	Litter Size (N)	-0.162	0.02	207
	Endemic	-0.091	0.193	207
	Climate Niche Breadth	0.05	0.472	207
	Habitat Breadth	-0.082	0.241	207
	Diet Breadth	0.06	0.394	207

Table 4.13 Pearson's correlation coefficient tests between Vulnerability with its constituent variables and body mass

The maintenance of correlations between Vulnerability and the raw variables of Sensitivity and Exposure^L, and also with body mass, indicate that through the method of calculation used to construct the Vulnerability measure has ensured that Vulnerability remains relatable to its constituent parts (Table 4.13).

4.4 Discussion

This chapter has developed a method of predicting species future Vulnerability to climate change and using this method it has explored future Vulnerability across Mammal Orders. It has also sought to identify those environmental and life history characteristics which predispose species to be Vulnerable, and those species, Orders and biogeographic zones biotas which possess these characteristics. The assessment of species future Vulnerability to climate change has been forwarded as a method which could aid the prioritisation of species found to be most at risk for conservation effort (Dawson *et al.* 2011). The forecasting of future risk to climate change requires knowledge not only of the degree to which a species is likely to be exposed to climate change but also the identification of traits which predispose the species to being susceptible to climate change (Fritz *et al.* 2009).

4.4.1 **Investigating Trends in Future Exposure to Climate Change**

Which species are most exposed under future climate change?

In this analysis 69% of species are predicted to experience range contractions this is less than the percentage predicted by Schloss *et al.* (2012) who predicted 87% of mammal species to lose range. However, Schloss *et al* only considered Western Hemisphere mammals, specifically those in North and South America, whereas this is a global analysis. There is large variation among regional biota and an individual taxon's susceptibility to climate change meaning that extinctions may be as low as 1% and as high as 80%. (Fischlin *et al.* 2007). This regional variation partially explains why the predicted figures for range contractions are not more closely matched. Projections of future global extinctions estimate that 20-30% of species experiencing 2-3°C warming above pre-industrial levels; will be increasingly at risk of extinction (Fischlin *et al.* 2007). Across the Mammals represented in the LHTd1084, 28% are predicted to lose over 50% of their current distribution by 2080 under a projected warming of circa. 2.4°C, tying in with IPCC projections.

There are 108 species predicted to lose above 80% of their current range by 2080 in the LHTd1084 of these only eight are represented in the LHTd213 and have associated Sensitivity data. There are 12 of the 108 species whose suitable climate space is predicted to shrink to below 10% of their current ranges, and which are considered extremely exposed. There are two species predicted to lose their entire range, the Desert pygmy mouse (*Mus indutus*) and the Pale Gerbil (*Gerbillus perpallidus*). The LHTd213 represents only two of the 'Extremely exposed' species (<10%), the red bellied titi (*Callicebus moloch,* Exposure^R=0.95) and the European bison (*Bison bonasus,* Exposure^R =0.08). The final 8 species completing this list include, in the Didelphimorphia, the Brown four-eyed opossum (*Metachirus nudicaudatus,* Exposure^R =0.91), in the Eulipotyphla, the Prebel's shrew (*Sorex preblei,* Exposure^R =0.04), the Macroscelidea, the Bushveld elephant shrew (*Elephantulus intufi*, Exposure^R =0.03) and five Rodentia species. These Rodentia are the Mexican volcano mouse (*Neotomodon alstoni*, Exposure^R =0.97), the Brown deer mouse (*Peromyscus megalops,* Exposure^R =0.93), the Philippine forest rat (*Rattus everetti*, Exposure^R =0.09), the Philippine pygmy squirrel (*Exilisciurus concinnus*) and the Belding's ground squirrel (*Spermophiulus beldingi*, Exposure^R =0.97). This analysis will refer back to these species at the close of this section to elucidate on the possible reasons for these species exhibiting heightened exposure.

Order

The Order to which a species belongs is shown to significantly relate to the degree to which it is likely to be exposed in the future, although the effect size is weak (ANOVA, Exposure^R, F (20, 1062) =1.837, p=0.01, η^2=0.03). This significant relationship is also evident in the LHTd213 (F (14,194) =1.686, p=0.06, η^2=0.10). It is possible that this relationship is a relic of past exposure. In Chapter Three Sensitivity was found to inversely correlate with past exposure with species having experienced a high velocity of climate change in the past being less Sensitive. Further, this theory predicts that a fingerprint of this past exposure will influence Sensitivity and be apparent in the degree to which species will be impacted by future climate change (Fritz *et al.* 2009). The Order to which a species belongs is significant in explaining between species variation across Sensitivity, thus, the relationship between Order and the degree of future exposure may be relatable to the fingerprint of past exposure on Sensitivity. A Pearson's product moment correlation coefficient was computed to assess the relationship between Sensitivity and Future Exposure^R. There is a modest, significant correlation between Sensitivity and Future Exposure^R (r=0.164, n=209, p=0.01). This would indicate that, as theorised, past climate change has left an imprint on current regional Sensitivity and this fingerprint will affect the degree to which species are exposed under future climate change.

Biogeographic realms and zonal exposure

Climate change is predicted to disproportionately negatively impact species within tropical zones (Beaumont *et al.* 2009). There is no suggestion that absolute temperatures (Δ˚C) will rise more in the tropics than in the temperate realm, however, it is hypothesized that future warming relative to past climate variability will be larger in the tropics (Beaumont *et al.* 2009). Thus, a small rise in temperature in the tropics is predicted to have a greater impact on tropical biota compared to the same rise on temperate species (Beaumont *et al.* 2009). Terrestrial species at higher latitudes, specifically in the circumpolar latitudes, are also thought to be disproportionately at risk in parallel with the rate of warming at these latitudes (Deutsch *et al.* 2008). Exposure^R values were not found to be significantly related to the realm, tropical or temperate, in which species occurred in both the LHTd1084 (ANOVA (F (1, 1077) =1.865, p=0.18) and within the LHTd213 (ANOVA, (F (1,207) =0.614, p=0.43). A possible explanation for this result lies in the fact that both tropical and temperate (circumpolar latitudes) are predicted to be at high risk under future climate change, although for different reasons as explained above. Therefore, at the geographic scale of realm ANOVA is unable to distinguish between the more subtle variations in exposure recognised at the scale of biogeographic zones. This variation can be observed in the exploration of exposure across biogeographic zones using ANOVA, Exposure^R was significantly related to zone in the LHTd1084 (F (6, 1070), p=0.00), a relationship which is preserved in the LHTd213 (F (6,202) =7.7, p=0.00). Results from zonal comparisons reflect the patterns of exposure predicted in the literature due to increased climate variability and to disappearing climate space and climate mismatches by identifying the Afrotropical, Neotropical and Oriental zones as harbouring the greatest percentages of species predicted to be most exposed to future climate change (Williams and Jackson 2007; Beaumont *et al.* 2009).

Ecological Factors linked to Exposure

Are there ecological factors which predetermine individual susceptibility to future climate change?

Disappearing climates are predicted to leave some species without suitable habitats with the probable result being their extinction (Williams, Jackson and Kutzbacht 2007). Thus, species extinctions are a likely consequence of climate change (Memmott *et al.* 2007). Several environmental factors are commonly identified as conferring high risk to future climate change, predicted to be manifested in future exposure values include range-restriction, narrow climatic tolerances and dispersal capacity (Beaumont *et al.* 2009). Species expected to be most at risk of extinction are those inhabiting mountain ecosystems, including montane tropical forests (Fischlin *et al.* 2007), and species which have already been exposed to other stressors, such as habitat loss (Williams and Jackson 2007; Williams, Jackson and Kutzbacht 2007). The fact that many populations are already threatened, means that any further loss of habitat associated with climate change will likely push these species to extinction (Fischlin *et al.* 2007).

Are climate specialists more at risk?

Functional limitations, related to a species environmental climate niche, are recognised as restricting the capacity to which species are able to adapt to novel climate conditions within their current range (Cahill *et al.* 2013). Thus, Climate specialists, species with narrow environmental climate niches are predicted to be at higher risk than species with more generalist requirements because they are restricted to inhabiting a limited range of possible climates by their tolerances (Kearney and Porter 2004; Dawson *et al.* 2011; Cahill *et al.* 2013). In the LHTd1084 219 species are defined as being climate specialists (Niche breadth<12.5%). Climate niche breadth has been observed to be preserved above the species level (Hadly *et al.* 2009), thus one might expect a relationship between Order and climate specialism. However, there is no relationship apparent between the Order to which a species belongs and the number of climate specialists species (ANOVA, F (20, 1083) =1.195, p=0.25).

In a comparison of climate niche and Exposure^{R} values across the LHTd1084, climate niche was found to be non-significant in determining future exposure (ANOVA, F (1, 1081) =0.017, $p=0.897$). Due to predicted regional climate variability this relationship was again tested across the biogeographic zones. The Afrotropical and Neotropical zones are the only zones with sufficient recorded climate specialists to test for whether climate specialism has an impact on future exposure. Between these zones neither was found to demonstrate a significant relationship between future exposure and climate specialism.

Are range-restricted species more at risk?

Extinctions and local extinctions are predicted to be especially prevalent among range-restricted species (Fischlin *et al.* 2007). There are 39 species classified as having restricted ranges (<250,000km^2,Ceballos and Ehrlich 2006) within the LHTd1084, equivalent to only 3% of the data. Within the data there is a significant relationship between Order and range-restriction (ANOVA, F (20, 1083) =6.045, p=0.00). This relationship has the potential to be used as an indicator of the impact of future climate change if range-restriction is valuable in predicting future exposure.

An ANOVA was run to test whether there is an association between range-restriction and future Exposure^R, the result was non-significant (F (1, 1081) =0.793, p=0.373) indicating that non-range-restricted species are equally susceptible to future exposure. However, range restriction was identified as significant in predicting future exposure when comparing within-zone variation using ANOVA. The Nearctic zone is the only zone which has sufficient records (n=22) to test whether exposure is predicted to be more severe amongst range-restricted species by region. A significant relationship was apparent between Exposure^R and range-restricted species (ANOVA F (1,291) =5.987, p=0.01), with range-restricted species correlating significantly with increased exposure (Pearson's one-tailed correlation, r=-0.194, p=0.00). This trend may not be apparent across the whole dataset because of the limited number of restricted-range species represented, an issue previously recognised by Warren *et al* (2013).

Are species which are range restricted and climate specialists more at risk?

Range restriction in combination with climate specialism has been identified as conferring heightened future risk to climate change (Thomas 2010). A significant relationship was identified between species which are both range-restricted and are climate specialists and future exposure (GLM, Exposure^R vs. (range-restricted*specialist), F (1, 1079) =9.53, p=0.00). Therefore, confirming the hypothesis that range-restriction and climate specialism in combination predisposes species to increased risk under future climate change.

Are endemic species more at risk?

Endemics may be disproportionately at risk from future climate exposure as many are range-restricted and have specialised climate requirements (Thomas 2010). There are nineteen endemic species predicted to lose above 80% of their current range by 2080 (Exposure^R=0.20), equivalent to 14% of the total endemics and 17% of the most exposed species. The Endemic species in the LHTd (n=131) are characterised as being more likely to exhibit narrow climate tolerance (ANOVA, F (1, 1081) =9.611, *p*=0.00) or to be range-restricted (ANOVA, F (1, 1081) =73.57, *p*=0.00), confirming the above statement. However, no link was found in the data to suggest that they were significantly more likely to exhibit both characteristics (GLM, Endemic vs. (range-restriction* climate specialist) F (1, 1079) =2.21, *p*=0.13), a prerequisite for explaining why endemics are predicted to be more at risk than other species to future climate change. Thus, it is of no surprise that there was not a significant relationship between whether a species is endemic and the degree to which it is predicted to be exposed (F(1,1081)=0.04, *p*=0.947). Despite the fact that restricted range and climate specialism were both found to explain within group variation between endemics and non-endemics, few endemic species display both of these characteristics, and in isolation neither were found to adequately account for greater risk to future climate change among the species represented in the LHTd1084.

Across the group of twelve species categorised as 'Extremely Exposed' six species occur within regions demonstrating the largest degree of climate change. These regions, the Neotropical, Afrotropical and Oriental each hold two of the six species. As previously discussed, species occurring in regions predicted to experience high climate change are more at risk because they are unable to keep pace with such rapidly changing and novel climate space. Four of the Nearctic species and the single Saharo-Arabian species, the Mexican volcano mouse (*Neotomodon alstoni*), the Brown deer mouse (*Peromyscus megalops,* Exposure^R=0.03), and the Belding's ground squirrel (*Spermophiulus beldingi*), and the Saharo-Arabian pale gerbil (*Gerbillus perpallidus*) are species which are both range-restricted and climate specialists. These factors have been identified in the literature as pre-dis posing species to large contractions in future climate space (Kearney and Porter 2004; Dawson *et al.* 2011; Cahill *et al.* 2013). The species unaccounted for by any environmental factor explaining their heightened risk to future climate change include the Palearctic European bison (*Bison bonasus*) and the Nearctic Prebel's shrew (*Sorex preblei*). Both the Prebel's shrew and the pale gerbil are identified as climate specialists, however this factor was not found to conclusively explain exposure risk. In the IUCN red list it is noted that the apparent rarity of the

Prebel's shrew may be an artefact of low sampling effort (IUCN) which could explain why it is determined as being extremely exposed. The European bison was re-introduced to some countries in Europe having been brought to the brink of extinction by hunting pressure it is now classified as Vulnerable by the IUCN (IUCN 2012) having low abundance which is reflected in its classification as having restricted range. This may explain the European bison's appearance amongst the 'Extremely Exposed'.

What characterize species which are predicted to thrive under future climate change?

It is theorized in the literature that some species will potentially expand their ranges into the future by colonizing geographical locations that duly fulfil their niche requirements (Colwell and Rangel 2009). There are 336 species, equivalent to 30% of the total species in the LHTd1084, predicted to maintain stable ranges or for which suitable climate space expands in the future under climate change (Exposure^{R}>1). Within the 336 species there are 270 species which are projected to expand their potential distribution above 10% and 76 of these above 50%.

One ecological-based argument for explaining these projected species expansions are related to the observations of the effect of recent climate change. Namely, that species are colonizing previously 'cool' regions, as environmental conditions begin to fall within their environmental niche requirements; a phenomenon already observed in the arctic, where arctic specialists ranges are contracting and temperate species expanding (Parmesan and Yohe 2003). Large-range size and broad environmental climate tolerances have been cited as being a factor supporting resilience to climate change (Williams 2008). Thus, the following his section examines whether either factor can be identified as playing a role in facilitating species range expansion under future climate change.

Are large range species more resilient?

There are 290 species which ranges larger than 4000000km^{2} (representing the upper quartile of the distributions in the LHTd1084). There are 75 species classified as predicted to expand their ranges above 10% of their current range which also have ranges categorized as large, 27% of the total number of expanding species, which is a small proportion of all those species projected to expand. Large range was found not have a significant relation to future exposure values (ANOVA, (F (1, 1084) =2.453, *p*=0.118)), and no correlation was found between future Exposure^{R} and large range size (one-tailed, r=-0.48, *p*=0.18). Significant relationships were reported between large-ranged species and Exposure^R values for the Afrotropical (ANOVA, F (1,245) =4.281, p=0.04) and Palearctic zones (F (1,105) =4.411, p=0.03) the two zones with sufficient records (>30 samples per group, (Cohen 1988)), with range sizes negatively correlating with loss of future suitable climate space ((Afrotropical, r=-0.13, *p*=0.04), (Palearctic r=-0.132, *p*=0.03)). These results could indicate that large range species are better able to cope with disturbances in regions where the degree of warming is large or climate variability is widespread. The climate in the Afrotropical zone is projected to change a great deal with large parts of the region predicted to experience changing and novel climates (Williams, Jackson and Kutzbach 2007). The Palearctic zone is predicted to experience the largest degree of absolute warming (Deutsch *et al.* 2008). However, without being able to test for this relationship across the remaining zones it is difficult to say whether this finding is robust.

Are climate generalists more resilient?

Species which can exploit an extensive range of climates due to a wide niche breadth, climate generalists, are predicted to be better able to adapt to future climate change because they are able to exploit a wider range of climate space (Williams *et al.* 2008). Species determined as climate generalists (Niche breadth=>0.5, n=86) were found not be significantly less exposed than other species (ANOVA, (F (1, 1081) =1.913, *p*=0.167). This analysis could not be assessed at the level of biogeographic zone as no region has sufficient records.

There was no link found between future exposure and climate generalism and large-range in combination (GLM, Exposure^R vs. (climate generalist* large-range) F (1, 1080) =2.381, *p*=0.12) suggesting that these traits do not confer resilience to future exposure or increase the likelihood that a species will expand its current range.

To conclude this section although no role was found for climate niche specialism or, range-restriction in isolation in explaining variation in future levels of exposure across species, in combination species which are both range-restricted and have narrow climate tolerances were found to be more at risk than those exhibiting one or neither characteristic. This conclusion ties in with trends evidenced in the literature (Thomas 2010). Endemic species represented in the dataset were not found to be more at risk from future climate change, although this is likely to be related to the fact that not all species termed endemic are range-restricted and climate specialists, factors cited as conferring endemic species particular susceptibility (Thomas 2010).

4.4.2 Is there a signal of regional past exposure apparent in the Sensitivity measure?

If the 'Ghosts of Species Past' theory (Fritz *et al* 2009) is correct then one would expect species Sensitivity to vary across zones in relation to variation in past exposure (see Chapter Three Section 3.4.3). Differences in Sensitivity across biogeographic zones were not tested for in the previous chapter. In agreement with the theory a significant difference in the distribution of Sensitivity is apparent when tested against biogeographic zones in the LHTd213 (ANOVA, F (6,202) =4.11, p=0.00). During the most recent episode of past climate change the temperate regions, particularly the Nearctic and Palearctic zones into which glaciers extended during the LGM, experienced the greatest velocities of past warming (Fritz *et al.* 2009; Sandel *et al.* 2011; Turvey and Fritz 2011). This hypothesis is confirmed within the data where the Neotropical and the Afrotropical zone have the largest percentages of most Sensitive species (Sensitivity=10>) within the zones species pool (Neotropical zone= 82% and Afrotropical zone=70%). The Nearctic and Palearctic zones have the least percentage of most Sensitive species, 63% and 53%, of each zones species pool, respectively.

4.4.3 Investigating patterns of Species Vulnerability to Future Climate Change

Which species are identified as being highly Vulnerable?

The species determined as being the most Vulnerable species is the Brown-mantled tamarind (*Saguinus fuscicollis*, Vulnerability=1.58) and the least Vulnerable the Cotton Mouse (*Peromyscus gossypinus,* Vulnerability=-0.39). Across the top 10% of Most Vulnerable species there are six common to either the top Most Sensitive or top Most Exposed species. Those included from the top 10% most Sensitive include the Tufted capuchin (*Cebus paella*) and the Brown bear (*Ursus arctos*). The remaining four belonging to the 10% Most Exposed, include the European bison (*Bison bonasus*), the

Brown- mantled tamarin (*Sanguinus fusicollis*), the Common mole rat (*Crymptomys hottentotus*) and the Giant Anteater (*Myrmecophaga tridactyla*). Those species in the top 10% which don't appear in the top 10% of most Sensitive or most Exposed include the Fennec fox (*Vulpes zerda*), the Striped polecat (*Ictonyx* striatus), the Grey Squirrel (*Sciurus carolinensis*), the Rock Hyrax (*Procavia capensis*), the Least Chipmunk (*Tamias minimus*) and the Cape ground squirrel (*Xerus inauris*). Therefore, it can be concluded that these remaining species appear among the top 10% most Vulnerable due to a combination of High Sensitivity scores and High future Exposure.

What determines future Vulnerability to Climate Change?

Disturbance, Resilience and the r-K Continuum

In the previous chapter Sensitivity was found to robustly relate to the characteristics theorised to support resilience, with species having a short life span, high reproductive capacity and fast life history (Williams *et al.* 2008), having low Sensitivity. In contrast those species identified as 'Highly sensitive' are characterized by 'slow' or *k*-selected traits, such as low reproductive capacity, having narrow diet and habitat requirements.

Importantly the Order to which a species belongs is significant in explaining variation within the Vulnerability measure (ANOVA (F (14,192) =2.554, *p*=0.00). The most vulnerable Orders, those with largest percentage of their total species richness occurring within the upper quartile of Vulnerability scores, include the Artiodactyla (Total richness= 21, Most Vulnerable=52.4%), the Carnivora (Total richness=56, Most Vulnerable=32.1%) and the Primates (Total richness=11, Most Vulnerable=27.7%). The least vulnerable Orders, those which have the large percentage of their total species in the lower quartile of Vulnerability scores, include the Lagomorpha (total richness=5, Least Vulnerable=80%) Didelmorphia (total richness=5, Least Vulnerable=60%), Chiroptera (n=24, Least Vulnerable=37.5%), and the Rodentia (total richness=59, Least Vulnerable=33%). These patterns of most and least Vulnerable Orders reflect the pattern within the Sensitivity measure.

Is climate niche significant for determining vulnerability?

As previously highlighted, Climate specialists, species with narrow environmental climate niches are predicted to be more vulnerable to future climate change because they are less able to adapt to climate variability, restricted to inhabiting a limited range of possible climates by their tolerances (Williams *et al* 2008). Generalist species (Climate niche breadth=50%>), however, were not found to be less Vulnerable than the average species (ANOVA (F (1,205) =0.131, *p*=0.718). Thus, climate niche breadth is a poor indicator of species future vulnerability.

Is restricted range relatable to vulnerability?

As previously discussed, climate change is also predicted to disproportionately affect range-restricted species (Thomas *et al* 2004). Unfortunately, there are no range-restricted species (<250,000km^2) represented in the LHTd213 to test whether this relationship is apparent across future Vulnerability scores. So, this analysis is unable to confirm whether range-restricted species are disproportionately at risk from future climate change.

Is Endemism relatable to Vulnerability?

Endemism has been linked to increase Vulnerability, particularly with regards to species' future exposure. However, within both the LHTd1084 and LHTd213 endemicity was not found to significantly contribute to explaining future Exposure^L. Further, within the LHTd213 endemism was not found to significantly explain variation in future Vulnerability (ANOVA, F (1,206) =1.70, *p*=0.19). However, within the LHTd213 there are few endemic species represented (n=11), and these are species which are not range-restricted or isolated on islands, traits determined as conferring endemics with their high vulnerability (Thomas 2010). Thus, this analysis is unable to measure robustly whether endemism confers heightened Vulnerability.

Does Vulnerability to future climate change vary spatially?

There is predicted to be regional variability in the degree to which species are Vulnerable to future climate change on account of both past sensitivity filtering and future predicted exposure (Beaumont *et* al 2010). To aid interpretation of global patterns of variation in future vulnerability and variability in the constituent Exposure^{L} and Sensitivity measures a series of maps (Figure 4.22) were created illustrating a) Future Vulnerability (most vulnerable as a percentage of total mammal species richness, b) Exposure (most exposed as a percentage of total species richness) and c) Sensitivity (most sensitive as a percentage of total species richness). Figure 4.22(d) illustrates total species richness across the LHTd213. Total species richness in this case refers to the number of species analysed in this research (Total species richness=213)

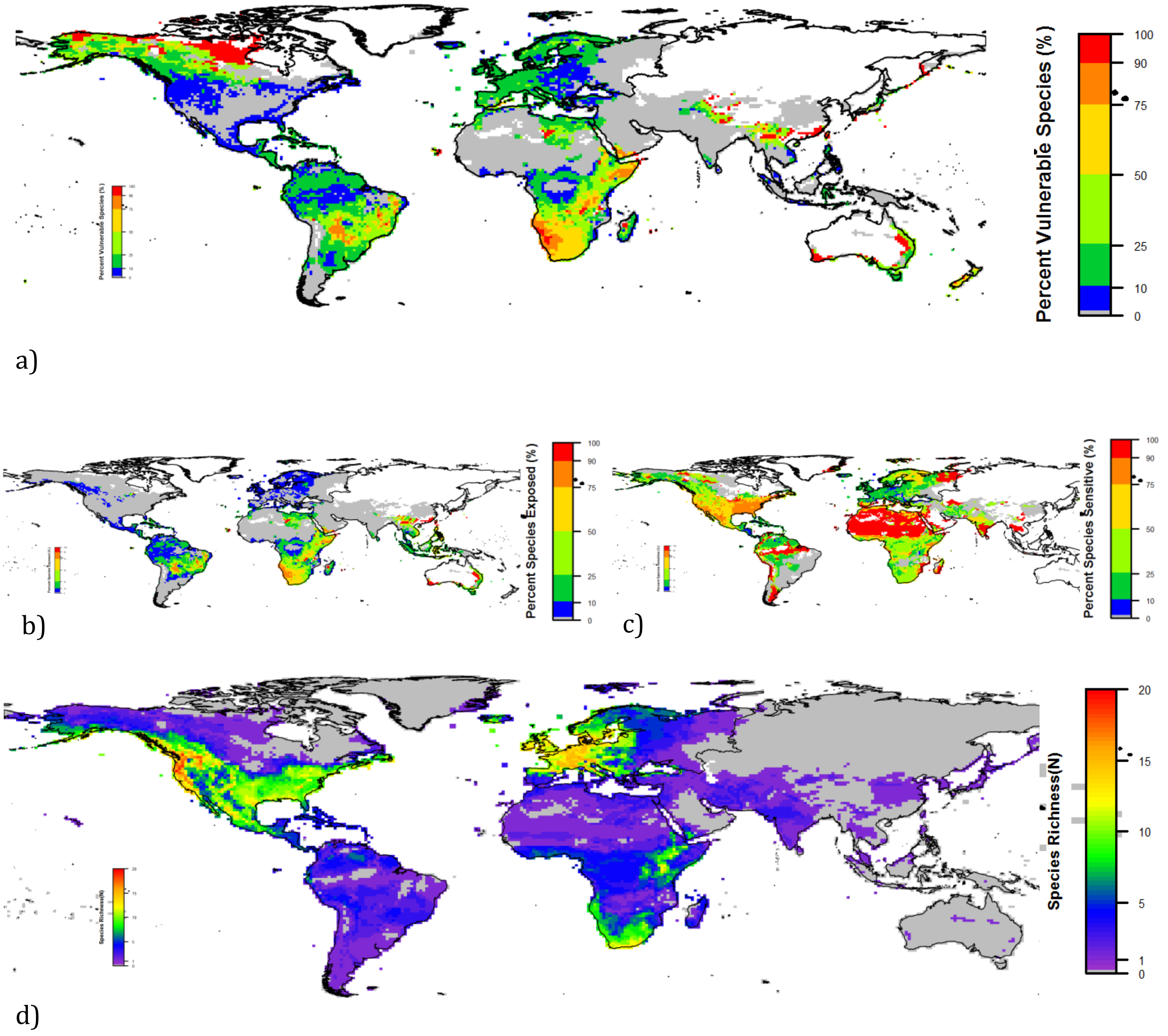


Figure 4.21 a) Vulnerability map (% most Vulnerable b) Exposure map (% most exposed), c) Sensitivity map (% most Sensitive), d) Species Richness map

Vulnerability was found to be significantly attributable to biogeographic zone when accounting for within Order variation (ANCOVA, F (7,199) =2.55, p=0.00). The Afrotropical zone has greatest percentage of species classified in the most Vulnerable category (Vulnerability=U.Q>) with 54.1% of the total species pool falling into this classification (Table 4.13). This pattern is reflected in the Vulnerability map (Figure 4.22a) which shows that between 50-75% of species represented in this region are classified among the most Vulnerable. The Palearctic zone has the next largest percentage, 36%, followed by the Neotropical zone with 26.5% of the species pool within the Most Vulnerable category. The Nearctic zone has the lowest percentage of species categorized as most Vulnerable at 9%, and this detail is apparent in the Vulnerability map (Figure 4.22a), where the major part of the region is shaded grey which represents no vulnerable species present. These results tie in with the results of Foden *et al* (2013) who found that birds of the Amazon basin and eastern South America, Europe, the Congo basin and parts of North America were particularly Vulnerable under future climate change. Amphibians were also found to be Vulnerable to climate change in Eurasia, southern North America to Mesoamerica and Madagascar (Foden *et al.* 2013) .

'Colonist' Species and Climate Change

There are several recognised traits that are common among 'colonist' species, for example they are mainly generalists; having broad dietary and habitat niches (Rödder and Weinsheimer 2009), and they often have a high reproductive rate, are fast growing and are successful dispersers (Vitousek *et al.* 1996). Whether a species is a climate generalist or not was found not to significantly explain variation across Vulnerability scores (F (1,205) =0.13, *p*=0.71), with 8 of the 25 climate generalists in the dataset (32%) being amongst the top most Vulnerable species.

In the previous section on the resilience of large-ranged species to Exposure, large range size was found to significantly relate significantly to the species potential for range expansion. There are 74 species classified as having large ranges (4000000km^2>) within the LHTd213, of these 21 are projected to expand their ranges by above 10% under future Exposure^L. However, large range was not found to be significant in explaining variation in future Vulnerability (ANOVA, F (1,205) =0.451, p=0.51). In fact of 66% (n=14) of the species classified as having the largest ranges are amongst the most Vulnerable.

Thus, species with large ranges currently or generalist tendencies are no more or less vulnerable to future climate change than species with smaller ranges and more specialist tendencies.

Predicting Vulnerability for an Iconic Species

Climate change has been attributed as a direct factor in increased endangerment for relatively few species,(IUCN 2009). One of the species represented in the LHTd213 is the Arctic fox (*Vulpes lagopus*). The Arctic fox is considered to be a good indicator of the overall health of the tundra ecosystem as one of the top land-dwelling predators (IUCN 2009). Thus, projecting the impact of future climate change on the fox is of special interest. Warming is predicted to affect the fox in three ways, i) range reduction, ii) increased competition with the red fox (*Vulpes vulpes*), and iii) fluctuations in prey availability (IUCN 2009).

Range reduction is predicted because the high latitudes, in which the Artic fox is found, are predicted to experience the greatest degree of absolute warming (Fischlin *et al.* 2007). The Artic fox is projected to lose 41% of current suitable habitat by 2080 (Exposure^{L}=0.41), reflecting the trend northward already observed in response to recent climate change (IUCN 2009). The Artic fox is an obligate carnivore with a comparatively long life span (mean longevity=15 years), a short gestation period (53 days) and a single large litter each year (mean litter size=7), being neither strongly *r*- or *K*- selected and this is reflected in its Sensitivity score (Sensitivity=9.90), which is close to the mean Sensitivity value across the LHTd213. The average Vulnerability score is 0.78, the Artic fox, as a result of the degree to which it is predicted to lose suitable climate space has a Vulnerability score of 0.98, although it is not among the most Vulnerable (Vulnerability=1.05>) due to its Sensitivity traits it is more vulnerable than its nearest relative the red fox (Vulpes vulpes, Vulnerability=0.81). Interestingly, the Artic fox’s nearest competitor, the red fox, is projected to increases its range northward, to partially overlap the future range of the Arctic fox by 2080 under the SRES A1B scenario (Wallace Initiative 2013). This would have the effect of increasing the Arctic fox overall vulnerability due to competition. The Vulnerability measure does reflect the broad trends predicted by the IUCN in terms of future exposure and adaptive capacity but cannot capture additional more localised interactions.

4.4.4 **Justification of methods and caveats**

Which additional factors are theorized to predict Vulnerability?

There are several additional factors considered to be important in the prediction of vulnerability unaccounted for by the Vulnerability measure. The full set of factors judged to be important in determination of future vulnerability are described in the Vulnerability framework (Williams *et al.* 2008), a summarized version of which is illustrated in Figure 4.23.

Factors assessed as being important in the measurement of Sensitivity, which are omitted in this analysis include: i) genetic diversity and inbreeding susceptibility, ii) population dynamics and minimum viable population size, and, iii) genetic, ecological and phenotypic plasticity. Each of these factors and reasoning behind their omission are discussed in further detail in Chapter Three.

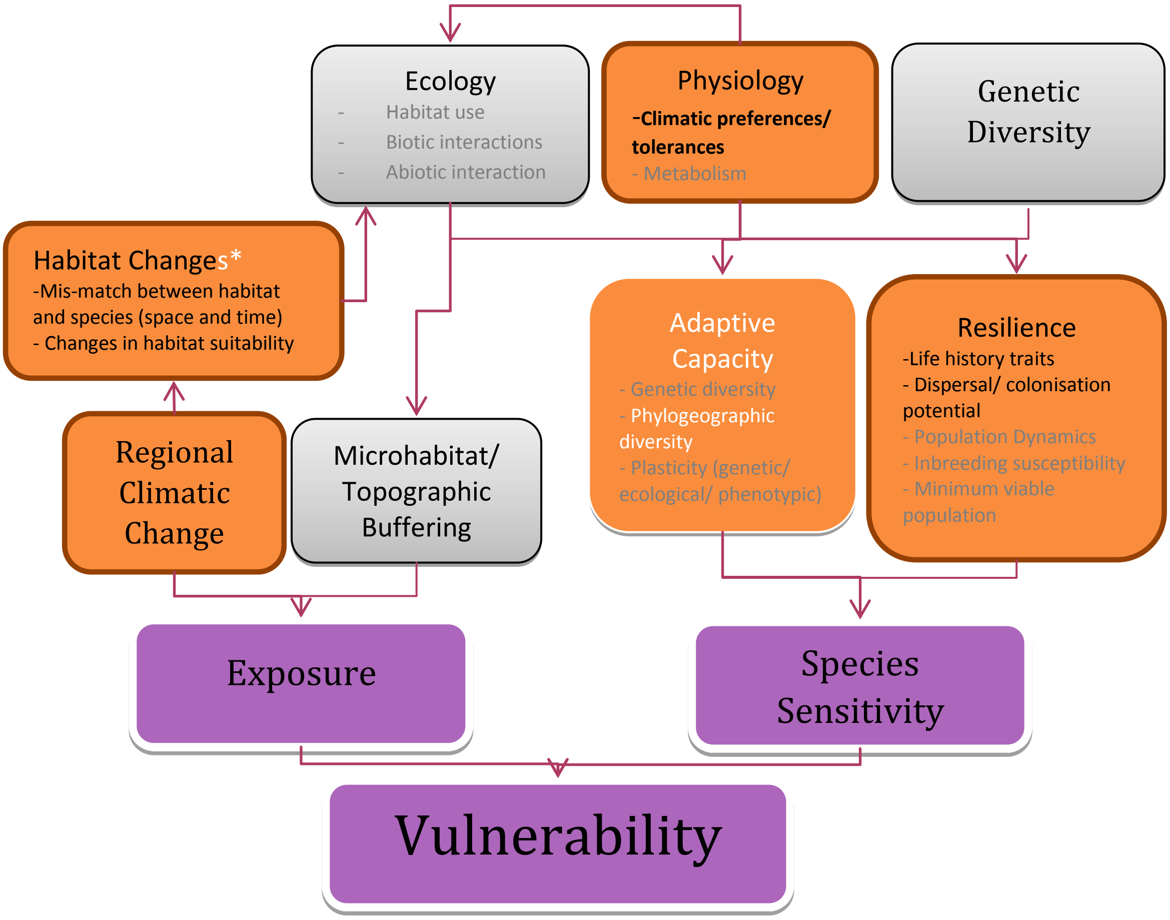


Figure 4.22 Summarized Vulnerability Framework (after Williams et al 2008) white text signifies factors accounted for in the Vulnerability measure.* Only partial representation as concerned with climate variation only

There are also factors relating to the measure of future Exposure which are not accounted for in this analysis of Vulnerability. These factors include i) Ecological factors such as, habitat use, biotic and abiotic interactions, and, iii) micro-habitat and topographic buffering. However, micro-habitat and topographic buffering and biotic interactions are not hypothesized to affect the distributions of species at the global scale (Pearson and Dawson 2003). Topographic elements are theorized to take effect at the regional to local scale and biotic interactions at the local to micro scale (Pearson and Dawson 2003, see Appendix One: Model Appraisal Appendix). Abiotic factors such as soil type are also theorized to play a role in determining species distribution but at the local and site level (Pearson and Dawson 2003). Thus, in an analysis of Vulnerability looking for patterns at the global scale, importance is negligible. It important to recognise that these factors will however influence the application of vulnerability analysis to species assessment below the global scale and need to be considered when seeking to apply knowledge gathered in this analysis to in real world situations.

Caveats associated with the calculation of Vulnerability

There are several widely acknowledged caveats associated with species distribution modelling, which are broadly related to, i) uncertainties in the model process and the requisite data, ii) incomplete representation of biotic and abiotic factors, and iii) extrapolation of current conditions to the future. These are further discussed in Appendix One the Model Appraisal Appendix.

With regards to this particular analysis uncertainty in projections is introduced in, i) the creation of the initial climate representation, ii) in the projections of future distributions and the associated dispersal mechanism, iii) incomplete representation of global mammal species richness.

First, with regards to the creation of the initial climate representation created to describe the species climate niche using Maxent. As discussed in the Maxent case study (Appendix Two: The Wallace Initiative Model and Species Distribution Modelling Techniques) selecting the most appropriate set of environmental variables is key to the prediction of the species niche (Phillips and Dudik 2008). The modelling process needed to be automated in order to facilitate the creation of thousands of individual species distribution predictions in the Wallace Initiative (Warren *et al.* 2013). There is no mechanism in the Maxent model to automate the selection of the most appropriate variables when iterating through species. This necessitated the selection of a set of climate variables which are widely accepted as being important in the definition of a large number of specie's distributions (Warren *et al.* 2013). Therefore, the environmental variables in the fixed set may not characterise the species climate niche as accurately as those selected by Maxent filtering into uncertainty around the predicted distribution. In the Maxent case study (illustrated in Appendix Two) the contribution of individual variables in describing the climate niche of the Common Frog was investigated. This analysis showed that during the process of variable selection only four of the pre-determined eight variable set defined by the Wallace Initiative appeared in the top eight most descriptive variables. Four environmental variables were better suited to describing the species niche. There is no measure of the degree to which having a proxy-variable set compared to the Maxent selected set affected the final distribution. However, it is likely that using a more simplified set of variables results in a less nuanced prediction leading to under or over-estimation of the final distribution.

This uncertainty could be narrowed by running Maxent for a representative set of individual species from each taxonomic group allowing the model to select the most salient variables. Then on the basis of these to create a bespoke set of variables for each taxonomic grouping.

Further relating to the representation of climate is the uncertainty rooted in the initial representation of the climate system by the GCM. Inconsistency in the GCM outputs stems from the mechanisms used to represent climate and future climate (Beaumont *et al* 2008). The degree to which alternative GCMs projections agree is both spatially sensitive, with some regions showing higher agreement than others, and temporally explicit, uncertainty widens the further from current conditions projections strayed (Wiens *et al.* 2009). The impact of this inconsistency in model projections filters into the projections of species distributions particularly future distributions. Regional uncertainty is particularly apparent in the Neotropical region due to the ability of individual GCMs to accurately represent the el Niño and la Niña weather systems leading to disagreement in the degree of future warming and changes in precipitation. In the case of the Wallace Initiative climatic uncertainty is narrowed by the use of an ensemble of seven GCMs, each of which is utilised to drive a projection of the individual species future distribution (Warren *et al* 2013). The mean of this ensemble of projections is then taken to represent the species distribution. Uncertainty in GCMs is further discussed in Appendix 3: Visualising Climate Change.

One particular caveat in the model is the nature in which the dispersal mechanism is represented. In the projection of suitable future climate space for mammals dispersal is set at 1.5km/yr for all species. It is unlikely that all mammals will disperse at this rate. For instance, it is considered likely that many small-bodied mammals dispersal capacity will fall below this rate because of their tendency to follow more winding less direct dispersal pathways (Schloss *et al.* 2012) meaning the model will overestimate their potential to track suitable climate space. Whereas, the estimated dispersal capacity of a small deer was measured at c.2km/yr (Francl *et al.* 2010), equivalent to an underestimation of dispersal range of 40km over the 80 year period (2000-2080) meaning the prediction of future distribution is unduly restricted. However, data for individual species dispersal capacity is rare (Williams *et al.* 2008; Warren *et al.* 2013) and not accounting for dispersal in any form is a serious weakness (Heikkinen *et al.*

2006; Wiens *et al.* 2009). This under- or overestimation of dispersal capacity will affect the results by inflating or under calculating the percentage of species predicted to be at risk under future climate change. One way of reducing this uncertainty is to further research dispersal capacity across the taxonomic groups or more simplistically as a function of body size.

One further concern relates to the creation of the composite score. The arbitrary measures 'Sensitivity' and 'Exposure' are weighted equally as at present there is no *a priori* weighting scheme by which to judge the strength of influence of either component on the overall Vulnerability. Therefore Climate change Vulnerability scores should be viewed as relative measures meaning that comparison between this analysis and further studies using the method developed here would not be meaningful. Until further research can shed light on the relative contribution of Sensitivity or Exposure factors in determining Vulnerability equal weighting of both components will remain.

The representation of mammal species within the database presents a further caveat, species representation in the LHTd1084 and particularly within the LHTd213 is biased with species from the Northern hemisphere being far better represented than those in the Southern Hemisphere, with Australia and Madagascar being particularly depauperate. This lack of species representation is recognised as a consequence of disproportionate representation of Northern hemisphere species in both the GBIF database (GBIF 2013) from which occurrence data is collated and also within the life history dataset. This analysis has identified the Neotropical and Afrotropical zones as each harbouring a large percentage of the species identified as most Vulnerable. Therefore, the bias of records within the Northern Hemisphere is likely to lead to an underestimate in the percentage of species globally likely to be classified highly vulnerable. The only method by which this source of uncertainty can be narrowed is by the collection of further locational and life history data concentrating on those gaps in species representation.

These caveats each require careful consideration when interpreting the findings of this research with no one caveat more important than the other. Issues relating to the difficulties surrounding the prediction of future climate change on species distributions are widely documented and discussed in further detail in the Appendices which cover caveats concerning species distributions modelling (Appendix One), the Maxent Model and the Wallace Initiative (Appendix Two) and predicting climate change (Appendix Three). These caveats being commonly recognised leaves the questions surrounding data paucity and the creation of the composite score. When making conclusions based on the results of this analysis one should be fully aware of the regions for which data availability may serve to limit our understanding of the degree to which species are vulnerable to future climate change. As an novel measure of future Vulnerability an effective form of statistical validity testing is currently unavailable meaning that comparison with the literature is the only way by which these predictions can be corroborated. No model is perfect (Pearson 2007) but without these analyses we are even less prepared for the possible impacts of climate change on biodiversity.

4.4.5 **Conclusions**

This chapter has explored the impact of incorporating Sensitivity and Exposure measurements into a single robust Vulnerability measure in order to assess the impact of future climate change on species. As identified in the introduction there is a lack of evidence to support the theory of Vulnerability, and further, that looks to identify which species are vulnerable to future climate change. Previous research on species vulnerability has been mainly hypothetical (Williams *et al.* 2008; Dawson *et al.* 2011), there is a single study (Foden *et al.* 2013) in the literature which has examined vulnerability in relation to climate change.

A criticism of previous analyses of global risk from climate change is that they fail to account for species' individual susceptibility to climate change (Thuiller *et al.* 2004; Kearney 2006). This analysis addresses this criticism by the inclusion of a measure of Sensitivity that weights the calculations, so that species with high exposure but low sensitivity are classified as less Vulnerable than those with high sensitivity and high exposure.

This study took a fundamentally different approach to determining vulnerability to that of Foden *et al.* (2013) specifically relating to the method by which species sensitivity was determined. The method by which Foden *et al*. (2013) determine Exposure is more similar basing their measure on predicted changes in future temperature and precipitation changes and their impact on habitat suitability. Foden *et al*. (2013) sought expert opinion on a wide variety of variables which they identified as contributing to species sensitivity (in the paper referred to sensitivity and adaptive capacity) these included 'rarity', 'habitat specialization', 'interspecific interactions', 'environmental tolerances' and 'dispersal ability'. They then assessed each species traits against thresholds determined in the literature to indicate high or low vulnerability and where these were not available thresholds were determined based on the range of values for each trait among the species analysed. In the absence of the resources required to gather experts together to collect information on perceived sensitivity and adaptive capacity traits this study enlisted statistical techniques PCA and regression analysis (see Chapter Three). Foden *et al.* (2013) categorised 24-50% of birds and 22-44% of amphibians included in their analysis as most vulnerable, that is highly exposed and highly sensitive with low adaptive capacity and assuming optimistic or pessimistic extreme values for missing data respectively. Despite the differences in method these results as percentage of species analysed are comparable to that determined for the mammals, 37% of which were labelled most vulnerable. This similarity provides further confidence in the method used in this study to determine Vulnerability. The approach presented here, compared to that of Foden *et al.* (2013) would be comparatively simple to undertake for other taxon where life history data is available because it does not rely on expert opinion to inform the development of the Sensitivity component instead being built on statistically robust techniques.

This chapter also determined the biogeographic regions projected to experience high future climate variability, these include the Afrotropical and Neotropical zones and to a lesser extent the Palearctic and Oriental zone which harbour high percentages of sensitive species. This combination of factors indicates that species in these regions are particularly vulnerable to future climate change. Foden *et al.* (2013) examined spatial vulnerability of amphibians and birds identifying the Neotropical zone, specifically the Amazon, as a region of high climate change vulnerability due to the high proportion of vulnerable species occurring there. They also identified the Congo basin and northern Africa, the Himalayas and Sundaland (Indonesia, Malaysia and the southern tip of Thailand) and the north-eastern portion of North America as harbouring a large proportion of highly vulnerable bird species. For amphibians, additional regions of high vulnerability were identified as Mesoamerica, North Africa and the Himalayas. The regions identified by Foden *et al.* (2013) are largely in agreement with those identified in this study for mammals, where differences exist they are largely relatable to the paucity of data for those regions in this analysis. Few mammal species are represented in the Sundaland and North African regions and so forming conclusions for these regions in this analysis would be disingenuous. Widespread agreement between these two analyses relating to regional vulnerability further validates the approach used in this study to describe vulnerability. It also bolsters the recommendation that the Neoptropical and Afrotropical regions be the focus of future conservation policy.

5 The Impact of Mitigation on Species Vulnerability to Future Climate Change

5.1 Research Context

5.1.1 Climate Change and Climate Change Scenarios

21st Century Global Warming

During the period 1990 to 2005 global temperature was observed to rise at a rate of about 0.2°C per decade (IPCC 2007). Over the following two decades warming of around 0.1-0.2°C per decade is projected independent of the emission scenario. This is unavoidable or locked-in warming as a result of past emissions and is known as the emissions floor (IPCC 2007). Beyond this date the degree of warming is more specific to the particular emission scenario being projected.

There are around 20 classified greenhouse gases of which the major contributors to climate change are listed in Table 5.1.

		Mol fractions and their changes		**Radiative Forcing (Wm^{-2})**	
Gas	**Formula**	**2005**	**Change since 1998**	**(Wm^{-2})**	**1998 (%)**
Carbon Dioxide	CO_2	379±0.6513µmol/mol [ǂ]	+13µmol/mol	1.66	+13
Methane	CH_4	1744±1.8.nmol/mol	+11nmol/mol	0.48	-
Nitrous Oxide	N_2O	319±0.12nmol/mol	+5nmol/mol	0.16	+11
Chlorofluorocarbon*	CFCs	79>538pmol/mol	-13>+4 pmol/mol	0.002-0.17	-5 > +22
Hydrochloroflurocarbons*	HCFCs	3.9> 169pmol/mol	+2.4>+38 pmol/mol	0.001-0.002	+29- >+ 349

Table 5.1 Greenhouse Gases contributing to past to Climate Change (as listed in the IPCC AR4 (IPCC 2007)**)**

*grouped ranges

[Ł] µmol/mol = ppm = parts per million (10^6); nmol/mol = ppb = parts per billion (10^9); pmol/mol = ppt = parts per trillion (10^{12})

Climate Change Mitigation

On the basis of observations into the response of ecosystems and their constituent species to recent warming van Vliet *et al* (2006) recommended that attempts be made to constrain future climate change to 1.5°C above pre-industrial levels, limited to less than an increase of 0.5°C per century. To this end it is important to investigate the impacts of different levels of mitigation upon species distributions and vulnerability upon which this chapter is concerned.

The process of mitigation describes reductions in resource use and emissions through technological change; it encompasses the implementation of policies which reduce greenhouse gas emissions and enhance sinks (IPCC 2007). The capacity for mitigation is determined by the degree to which anthropogenic emissions can be curtailed and natural sinks can be enhanced and is dependent on information, wealth, infrastructure and technology (IPCC 2007). Thus, the mitigation potential is the amount of mitigation that could be achieved over time determined by economic, technical and market potential.

The use of idealized scenarios encompassing mitigation, facilitates the investigation of the impact of different levels of climate change on species' vulnerability helping to identify possible thresholds above which species are lost (Beaumont *et al.* 2008).

5.1.2 Climate models and Emission Scenarios

Climate models seek to represent the development of the climate system over time; as such their basis is rooted in the physical laws and recent observations of climate (Beaumont *et al.* 2008). A major part of this process is named the 'spin-up' period in which the model seeks to simulate the recent and current climate and to achieve equilibrium across the input components (Beaumont *et al.* 2008). At this point simulations of the future can be undertaken through the introduction of changes, for instance in greenhouse gas emissions. A key test of a model's ability to represent climate is whether it can simulate characteristics of the current climate as well as successfully replicate elements of the past and recent climate change (Beaumont *et al.* 2008).

In choosing the climate model and emissions scenarios appropriate for modelling future projections of species distributions one wishes to characterise the climate-related uncertainty associated with the output (Beaumont *et al.* 2008). There is not one single 'best' climate model; each will predict the climate slightly differently depending on the inputs (Beaumont *et al.* 2008). Variability between GCMs is introduced by the mechanisms employed to represent Earth system processes (i.e. hydrological cycle), the spatial and vertical resolution of climate processes and the number of climate feedback mechanisms involved (Meehl *et al.* 2007; Beaumont *et al.* 2008; Buisson *et al.* 2010). As such employing a suite of climate models (GCMs), as the Wallace Initiative does, not only reveals where uncertainty in climate projections lies but also helps to smooth this form of uncertainty (Beaumont *et al.* 2008). This form of uncertainty would have ramifications at the species level because under each GCM the extent of available suitable climate space and its geographic position shifts dependent on the GCM enlisted (Buisson *et al.* 2010). Buisson *et* al (2010) investigated the degree to which the GCM used increased variability in the projection of future species distributions. They found that GCM choice accounted for around 20% of total variability of species range change projections in 2080 equivalent to that introduced by the SDM for the same time period. As discussed in Chapter Four this method does reduce uncertainty across climate projections but not biological uncertainty which can only be reduced using ensemble modelling.

Emission Scenarios

Emission scenarios seek to define plausible storylines of future development in emissions such as greenhouse gases and aerosols. These are determined under alternative descriptions of the driving forces which contribute to emissions release such as technological advances, demographic and socio-economic development (IPCC 2007). These scenarios' trajectories are then input into models which project drivers of ecosystem change, the environmental variables, for use in biodiversity models (Pereira *et al.* 2010). In selecting a set of emissions scenarios it is important to represent the widest range of plausible climate change outcomes, from conservative to extreme (Beaumont *et al.* 2008). In the Wallace Initiative simulations of 6 alternative scenarios are examined representing at one end a business-as-usual (SRES A1B) strategy and at the other strict mitigation (A16r5l, (Gohar and Lowe 2009)). In order to allow easy comparison of the six scenarios the origins of these scenarios are outlined in further detail below.

IPCC SRES Scenarios

The SRES A1B scenario is one of a family of scenarios created for the IPCC encompassing alternative modes of development and the resulting greenhouse gas emissions. These scenarios project an increase in baseline greenhouse gas emissions of between 9.7 and 36.7 $GtCO_2$-eq this is equivalent to a 25-90% increase, between 2000 and 2030 (Pachauri and Reisinger 2007). Under all of the SRES scenarios the use of fossil fuels is predicted to remain dominant.

There are four major SRES scenario families, A1, A2, B1 and B2. The A1 storyline encompasses very rapid economic growth; the development of new and efficient technologies and a peak in world population mid-century, there are three sub-groups which describe alternative routes of technological development (Pachauri and Reisinger 2007). These subgroups are A1F1, A1T and A1B. A1F1 describes fossil fuel intensive technological change, A1T technological advancement using non-fossil energy resources and A1B which describes mixed usage of both fuel types. The B1 scenario describes a convergent world with the same global population but with more rapid changes in economic structure towards a service and information economy. The A2 scenario describes a storyline with high population growth, slow economic and technological change, whereas the B2 scenario describes a world with intermediate economic and population growth predicting more localised solutions to social and economic sustainability (Pachauri and Reisinger 2007). There is no one scenario described as being more likely than the others (Pachauri and Reisinger 2007).

AVOID scenarios

The AVOID scenarios are a series of mitigation storylines created through a collaboration headed up by the UK Met Office, which use the IPCC SRES scenarios as their basis (Gohar and Lowe 2009). There are three sets of scenarios which use the SRES A1B scenario as a baseline but which use different growth rates of emissions, timings of peak emissions and degrees to which emissions are reduced post-peak (Gohar and Lowe 2009). In this chapter a set of five AVOID emissions scenarios is used, with three representing peak emissions at 2016, embodying annual reductions in emissions thereafter of 2%, 4% or 5%, and two representing peak emissions at 2030, with annual reduction in emissions of 2% and 5%.

The Impact of Mitigation over time

Several studies have investigated the impact of different mitigation scenarios over time (Wigley *et al.* 1996; Yohe and Strzepek 2007). However, few studies have sought directly to compare the impacts of different mitigation scenarios on risk or vulnerability under future climate change (Foden *et al.* 2013; Warren *et al.* 2013).

This study will investigate the impact of different degrees of mitigation on species exposure over time, making comparisons within the literature, but also more distinctively it will look at the impact of mitigation on perceived species' Vulnerability over time.

5.1.3 Objectives

This chapter seeks to make comparisons across both the business-as-usual (SRES A1B scenario) and mitigation scenarios (AVOID) investigating the impact of mitigation by potentially delaying the negative impacts of climate change. In doing so we are better able to pinpoint the time period in which mammal species could be most vulnerable, and whether this varies across Orders and within biogeographic regions.

This chapter will address the following specific research questions:

- What effect does mitigation have on species overall Exposure levels?
- How does the level to which mitigation is implemented impact the future Vulnerability of species?
- Are there species for which mitigation has no impact on the degree to which they are Vulnerable?

5.2 Methods

This chapter seeks to investigate the impact that mitigation might have on species Vulnerability to future impacts of climate change as outlined in detail in this thesis.

5.2.1 Mammal Vulnerability and Data

Mammal Vulnerability scores are created by combining species' individual Exposure and Sensitivity scores to generate a composite score. Species' vulnerability is classified into five categories Extremely Vulnerable, Highly Vulnerable, Moderately Vulnerable, Lowly Vulnerable and Least Concern, see Chapter Four. The Creation of the Sensitivity Measure

This section is a brief outline of the calculation of the Sensitivity Measure which was calculated in the Chapter Three. Sensitivity is a composite score which represents a combination of 10 life history traits and ecological variables which explain variation across species and whose inclusion was determined by PCA. The ten life history and ecological variables are listed in the Table 5.2.

Life History and Ecological Traits	
Sexual Maturity (Days)	Litter Size
Longevity (Months)	Diet Breadth
Weaning Age (Days)	Habitat Breadth
Gestation (Days)	Endemic
Litters per year	Climate niche Breadth

Table 5.2 Sensitivity Measure Composite Life History and Ecological Traits

There are 213 species for which Sensitivity scores were created, representing 15 Orders and 58 families. The data for these species were extracted from the LHTd which was created using databases covering life history traits and ecological variables (Further details and references for which are in Chapter Three: Calculating Species Sensitivity). The scores range between least sensitive at 4.15 to most sensitive at 14.79.

5.2.2 Calculating Future Exposure by Emission scenarios

To measure the impact of alternative emissions scenarios on mammal species Vulnerability requires the calculation of Exposure^R under each scenario. Data for current and future projections of species distributions are created in the Wallace Initiative using the species niche model, Maxent (Phillips and Dudik 2008). These projections are based on species current distribution occurrence data (GBIF 2013) and a suite of 4 or 8 bioclimatic variables (Hijmans *et al.* 2005) dependent on the number of occurrence records. These predictions of current distributions are then projected under scenarios of future climate change created using CIAS (Community Integrated Assessment System (Warren *et al.* 2008)). CIAS brings together several Global Circulation Models (GCMs) projections of future climates. The method by which these projections are created is further detailed in Appendix Two: The Wallace Initiative and Species Distribution Modelling Techniques.

The Emission Scenarios

Table 5.3 illustrates numerically the differences across the emission scenarios in terms of Global mean temperature at 2100, the emissions decrease post peak, the emissions floors and also the probability of constraining any temperature rise to below 2°C.

Emission Scenario	**Global Mean Temperature by 2100 (°C)**	**Post peak emissions CO_2 emission decrease**	**Emissions Floor** ($GtCO_2$/yr.)	**Probability of constraining the temperature rise to below 2°C above pre-industrial levels**
Baseline SRES A1B	4.0	-	-	<1%
Mitigation 2030-2-h	2.8	2%	16	7%
Mitigation 2030-5-l	2.5	5%	6	17%
Mitigation 2016-2-h	2.2	2%	16	30%
Mitigation 2016-4-l	2.0	4%	6	44%
Mitigation 2016-5-l	2.0	5%	6	45%

Table 5.3 Global Mean Temperature by 2100 (°C) adapted from Warren et al 2013 & AVOID (Gohar and Lowe 2009)

Calculating Exposure over time

In the previous chapter the impact of climate change under the SRES A1B scenario was investigated at a static point in time, 2080. Climate impacts on species are only investigated this far into the future because of the increasing uncertainty associated with the climate models beyond this point (Warren *et al.* 2013).

To calculate the degree to which species are exposed over time to climate change, Exposure^R was calculated for time slices across the period Current to 2080. The time slots for which Exposure^R values were characterised are 2020, 2050 and 2080. These Exposure^R values are created under each of the Emission scenarios for comparison. The data for the impact of the alternative emissions scenarios on each species distribution over the time slices were provided by the Wallace Initiative (Wallace Initiative 2013). These data are in the form of current and future distribution area (km^2) for each time period by each emission scenario by each GCM. There are thus 42 projections created for each time slices (six emissions scenarios x seven GCMs) apart from the current for which there is only one prediction created as it is based on observations. There are seven projected distributions for each species for each future time slice one for each GCM. It was necessary to run the GCMs in the Wallace Initiative as they had not been run for the AVOID emission scenarios previously (Warren *et al* 2013). To create a single projection of absolute climate change the median of the GCMs is calculated and used to drive the pattern-scaling module ClimGEN, part of CIAS (Warren *et al* 2006). This model combines the scaled climate change patterns determined by the GCMs and then combines the projection with baseline climate (1961-1990) to create the environmental variables (Warren *et al*. 2013). There are several methods for combining ensemble outputs such as taking the mean, median, accounting for the range (Jones *et al.* 2013), or weighting each GCM contribution to the final combined projection by how well it reproduces the observed climate (Sansom *et al.* 2013). Jones *et al* (2013) advised considering both the mean and the range of the projections, in this case for potential future species distributions, in order to understand uncertainty surrounding the 'best' and 'worst' case scenarios. In this analysis into the potential range of future climates predicted by the GCMs is undertaken in Chapter 5 Section 3.3. and Appendix Three. With regards to the pattern-scaled climate change projections used here there is no method by which the relative merits of each GCM to predict future climate change can be expounded so weighting is not an option (Warren pers.comm). For an examination of the uncertainty across the GCMs see Appendix Three: Visualising climate change.

Figures of changing Exposure^R over time are then created across the full set of Mammal scores and subsequently for each of the Orders. These figures are created by calculating the mean Exposure^R score across the full set of species under each emissions scenario for each time slice. The minimum and maximum value of Exposure^R for each time slice and emission scenario is also recorded. The mean values of Exposure^R are then plotted for each emission scenario over time with the minimum and maximum values around the mean represented using shaded polygons.

5.2.3 Calculating Vulnerability by Emission Scenario

The further assessment of species' Vulnerability required the creation of a composite score to represent Vulnerability for each Emission scenario. The Exposure measure relevant to these calculations is Exposure^L. The Sensitivity score is held constant whilst the Exposure^L score calculated for each emission scenario is substituted into the equation by turn.

Therefore the final Vulnerability equation is:

$$Vulnerability = Sensitvity_N + Exposure^L\ (proportion\ loss)_{n*emission\ scenarios})$$

Where the N indicates that the variable has been normalized. The resulting Vulnerability scores range from least Vulnerable (-0.385) to most Vulnerable (1.585). The highest possible Vulnerability score is Vulnerability=2, a combination of high Exposure^L (100% loss of current distribution by 2080) and high Sensitivity (Sensitivity=14.79, normalized to 1). This assumes that equal weight is given to both Sensitivity and Exposure in the definition of Vulnerability.

5.3 Results

5.3.1 Exposure by Emission Scenarios

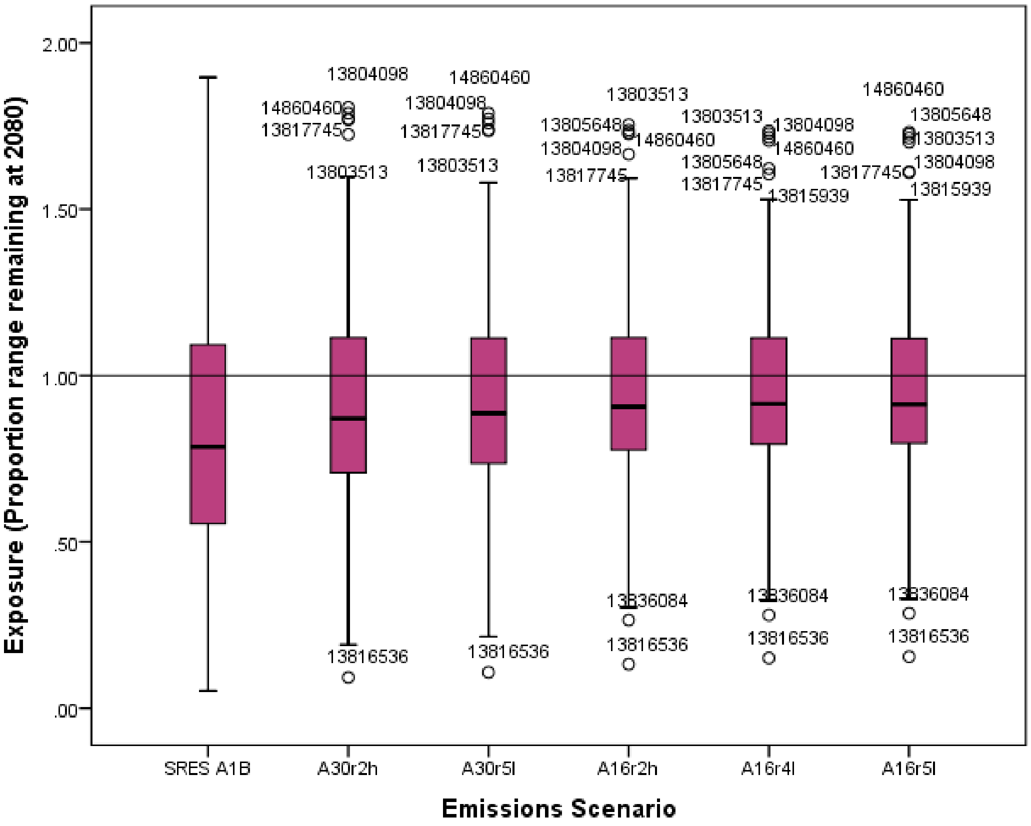


Figure 5.1 Boxplots of Future Exposure^R by Emission Scenario (Proportion Range Remaining at 2080) The line at 1.00 indicates that the distribution size remains stable, below which distribution contracts and above which expansion is predicted to occur. Outliers are indicated by species ID number.

Error! Reference source not found. is a boxplot of Future Exposure^R in 2080 by Emission Scenario and allows the exploration of Exposure^R values across the different scenarios. Under the no mitigation (business-as-usual) scenario, SRES A1B, species are predicted to experience an average reduction in distribution of 18% by 2080 (mean Exposure^R=0.82), by implementing the most stringent mitigation scenario (A16r5l) this is reduced to an average 7% loss (mean Exposure^R=0.93), protecting a further 12% of the specie's distribution into the future.

The greatest number of positive outliers, those which are predicted to be least exposed to future climate change, occur under the A16r4l and A16r5l, they include two Rodentia, and one of each of the following, a Eulipotyphla, Primate, Carnivora and Didelmorphia. Under the A16 scenarios there are two negative outliers, those which despite mitigation remain highly exposed to climate change. These species, both primates, are the endemic red-bellied titi (*Callicebus moloch*) and Brown-mantled Tamarin (*Saguinus fusicollis*).

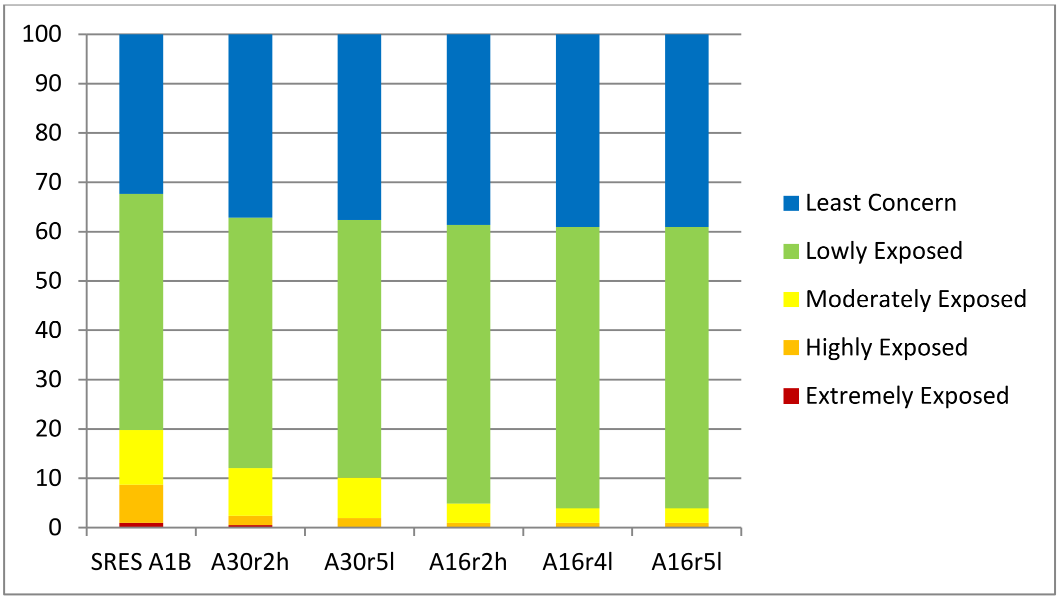


Figure 5.2 Classification of Exposure Across the Emission Scenarios (Percentage species by classification, Percentage loss classification; Extremely Exposed ≥90%, Highly Exposed 70%>90%, Moderately Exposed 50%>70%, Lowly Exposed 0%>50%, Least Concern indicates expansion)

The no mitigation (SRES A1B) scenario holds the largest percentage of species classified as Moderately to Extremely Exposed at 20% this drops to 4% under the most stringent mitigation scenario (A16r5l), a reduction of 16% (Figure 5.2). Under the two scenarios representing a peak in $C0_2$ emissions at 2030 only one species is predicted to be Extremely Exposed by 2080, the Red-bellied titi (*Callicebus moloch*), which is a monkey endemic to Brazil. The A16 scenarios (strict mitigation) have no species predicted to lose over 90% of their suitable distribution under future Exposure^R. Further the margin between species classified as 'Moderately to Extremely Exposed' across the three scenarios is small with between 3-5% of species in these categories from A16r2h to A16r5l.

The scenarios representing peak $C0_2$ at 2030 (moderate mitigation) predict that between 12% (A30r2h) and 10% (A30r5l) of species to be classified 'Moderately' to 'Extremely Exposed' by 2080, a reduction of between 8-10% of species in comparison with no mitigation (SRES A1B). Where peak CO_2 is achieved at 2016 (strict mitigation) the percentage of species classified as 'Moderately' to 'Extremely Exposed' is 4-5% (A16r5l and A16r2h). Thus, mitigation offers a 5-8% decrease in the number of species predicted to be Moderately to Extremely Exposed by 2080.

Exploring changing Exposure through Time.

To assess the impact of each emission scenario across all mammal species included in the LHTd213 the mean Exposure^R was calculated for each scenario over time (Figure 5.3). Minimum and maximum Exposure^R values were also calculated to illustrate the deviation in Exposure^R across the species.

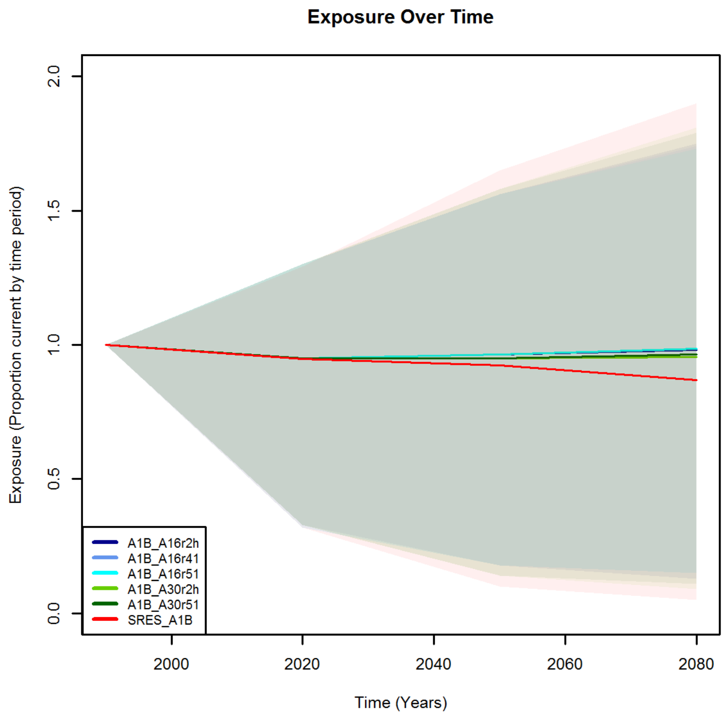


Figure 5.3 Exposure^R Over Time All Mammals (Proportion of current range remaining over time, coloured lines indicate the mean of each emissions scenario and corresponding coloured polygons the degree of variation in species distribution change under the relevant scenario.)

The Emission scenario indicating the highest loss in distribution to 2080 is that of No mitigation (SRES A1B) with an average range reduction of 18% by 2080, under this scenario the greatest loss in distribution is also predicted (95% loss) (Table 5.4). However, it is also the scenario under which the largest expansion in distribution is predicted with a 90% increase in suitable climate space. Further, the largest divergence in predicted range changes is also observed under the no mitigation scenario. The narrowest degree of variation between minimum and maximum Exposure^R is recorded for the Moderate mitigation scenario (A30r5l).

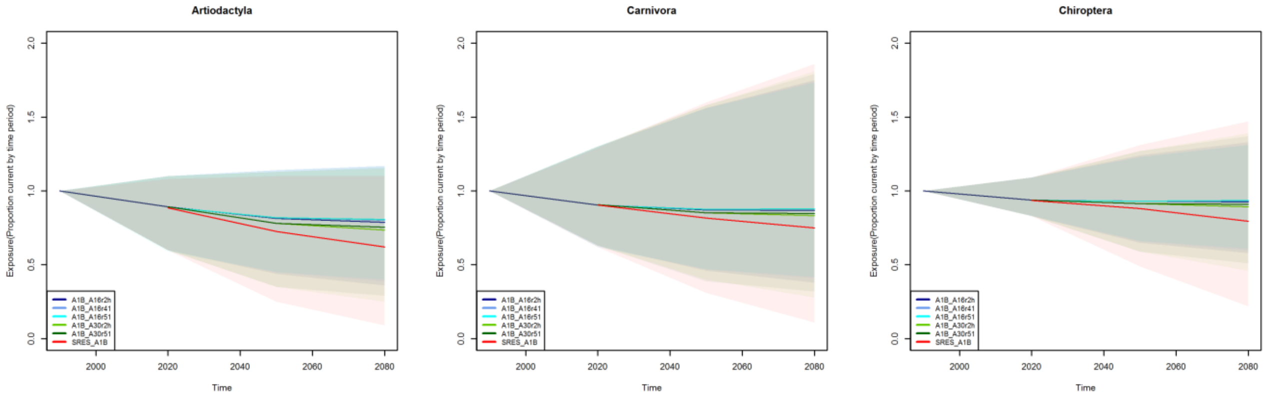
The smallest standard deviations in Exposure^R values are recorded for all emission scenarios at 2020 with the largest standard deviations for all scenarios at 2080. Levels of standard deviation at 2080 are equivalent to a 27% (Strict mitigation) and 39% (No mitigation) variation in distribution changes (Table 5.4). That predictions over this period harbour most uncertainty is unsurprising as the further projections move away from current conditions the less stable predictions become (Williams and Jackson 2007).

		Exposure (Proportion Range remaining)			
Emission Scenario	**Time Period**	**Mean**	**Maximum**	**Minimum**	**S.D**
Strict	2020	0.93	0.31	1.30	0.14
	2050	0.92	0.18	1.56	0.23
	2080	0.92	0.15	1.73	0.27
Moderate	2020	0.93	0.33	1.30	0.14
	2050	0.91	0.14	1.58	0.26
	2080	0.91	0.11	1.79	0.31
None	2020	0.93	0.32	1.29	0.14
	2050	0.87	0.10	1.65	0.29
	2080	0.82	0.05	1.90	0.39

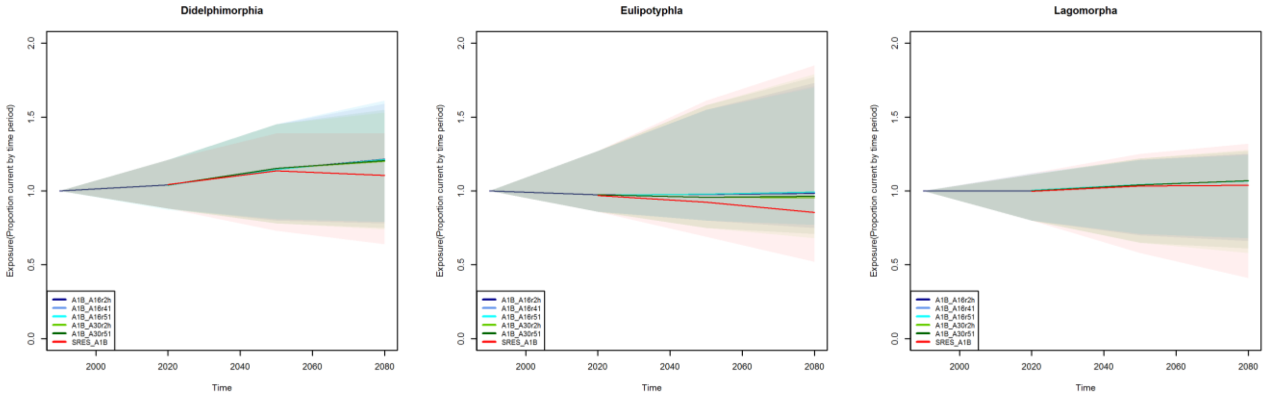
Table 5.4 Exposure over time by Emission Scenario

Over the time period 1990 to 2020 species are predicted to lose on average 9% of their range across all scenarios. During the period 2020 to 2050 further range loss is predicted under the no mitigation scenario with species predicted to lose an average 4% of their total range. Under moderate mitigation this further loss is narrowed to 2% and under strict mitigation a very narrow (1%) recovery is predicted. Exposure stabilises for both the Strict and Moderate mitigation scenarios in the period 2050 to 2080. Whereas, under the no mitigation scenario species are predicted to lose on average a further 5% of their total range.

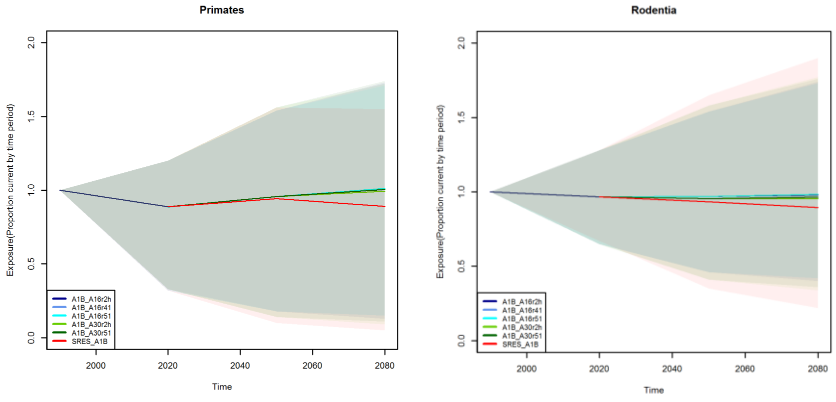
Exposure by Order over time



a) Artiodactyla b) Carnivora c) Chiroptera



d) Didelmorphia e) Eulipotyphla f) Lagomorpha



g) Primates h) Rodentia

Figure 5.4 Exposure^R over the period 1990-2080 by Order (a-h). Illustrating the changing levels of Exposure^R between the period 1990 to 2080 by Order under the suite of Emission Scenarios.

Further plots of Exposure^R were created to investigate the impact of the alternative emission scenarios across the Orders (Figure 5.4). The Order experiencing the greatest degree of mean Exposure^R across the whole suite of scenarios is the Artiodactyla

(Figure 5.4a), predicted to lose between 20% under the most stringent mitigation (A16r5l) to 38% under the no mitigation scenario (SRES A1B) by 2080. The Didelmorphia (Figure 5.4d) are the Order predicted to be least impacted by climate change, with a mean Exposure^R value of between 1.10(SRES A1B) to 1.21 (A16r5l) at 2080, an average increase in the range of 10-21%. The Primates (Figure 5.4g) include the species most adversely affected by climate change, predicted to lose between 95% (SRES A1B, Exposure^R =0.95) to 85% (A16r5l, Exposure^R =0.85) of its current range by 2080. The Order Carnivora (Figure 5.4b)contains the species predicted to be least impacted by future climate change across the full suite emission scenarios predicted to expand its range by between 85% (SRES A1B) and 73% (A16r5l) by 2080. The Rodentia (Figure 5.4h) hold the species predicted to expand its range the most under the SRES A1B scenario, the Round-tailed ground squirrel (*Spermophilus tertricaudus)* with a predicted expansion of 90% by 2080.

Under the A16r5l scenario the Orders Didelmorphia, Eulipotyphla, Lagomorpha, Primate and Rodentia were predicted to begin to recover or continue to expand their ranges during the period 2050-2080 by on average 1% (Eulipotyphla and Rodentia) to 7% (Didelmorphia). The Carnivora and Chiroptera' distribution extents are predicted to stabilise. The Artiodactyla are the only Order predicted to continue experiencing an average contraction in distribution size with a predicted average loss of a further 1%.

The Primates are predicted to lose an average of 12% of their range by 2020 under the scenarios. This trend reverses during the period 2020-2080 under the A30 and A16 scenarios with range expansions predicted of between 10% (A30r2h) and 13% (A16r5l). The picture under the SRES A1B scenario is less easily described with Primates predicted to expand their ranges between 2020-2050 by an average of 5% but to experience a complete reversal of the previous decade's expansion between 2050-2080, when they are predicted to lose and average of 5%. A similar pattern is evident for the Didelmorphia (Figure 5.4d). Although this does not entirely reverse the perceived expansion of 2020-2050, it does indicate a stabilising of distribution.

Under the full suite of emission scenarios distributions the Lagomorpha seem relatively stable across the entire period with very a slight increase in range projected of between 4% (SRES A1B) and 7% (A30s). This indicates that under even a moderate degree of warming the Lagomorpha are projected, on average, to expand their ranges resulting in a low overall Vulnerability.

5.3.2 **Vulnerability by Emission Scenarios**

The following section investigates the impact of mitigation upon species Vulnerability and looks across the six mitigation scenarios from business-as-usual (SRES A1B) to strict mitigation (A16r5l). In a GLM looking at the impact of emission scenarios on Vulnerability the relationship was found to be significant (F=5, 1236, *p*=0.00).

Figure 5.5 plots Vulnerability across the six emission scenarios. Vulnerability scores range between the most vulnerable at 1.58 and least vulnerable at -0.39 (Figure 1.5). The largest mean Vulnerability score is forecast for the SRES A1B scenario at an average of 0.76, falling to 0.67 under the A30r5l scenario and to 0.64 under the most stringent A16r5l scenario. The maximum Vulnerability score is predicted under the SRES A1B scenario at 1.58, under the A16r5l scenario this is reduced to 1.40. The lowest Vulnerability score is also predicted under the SRES A1B scenario at -0.39 rising to -0.19 under the A16r5l scenario.

The single species labelled as a positive outlier, Extremely Vulnerable to future climate change, under the A16r4l and A16r5l is the endemic Red-bellied titi (Vulnerability= 1.41-1.40). The species labelled as negative outliers, those predicted to be of Least Concern, across all scenarios are the North American species the Cotton mouse (*Peromyscus gossypinus*) and the Common kusimanse (*Crossarchus osbscurus*) native to West Africa. The Rodentia species the Round-tailed ground squirrel (*Spermophilus tertricaudus*) native to North America and northern Mexico is also classified as an outlier under the SRES A1B scenario. Under the A16r4l and A16r5l the Robinson's mouse opossum *(Marmosa robinsoni*) is also classified as an outlier and so of least concern.

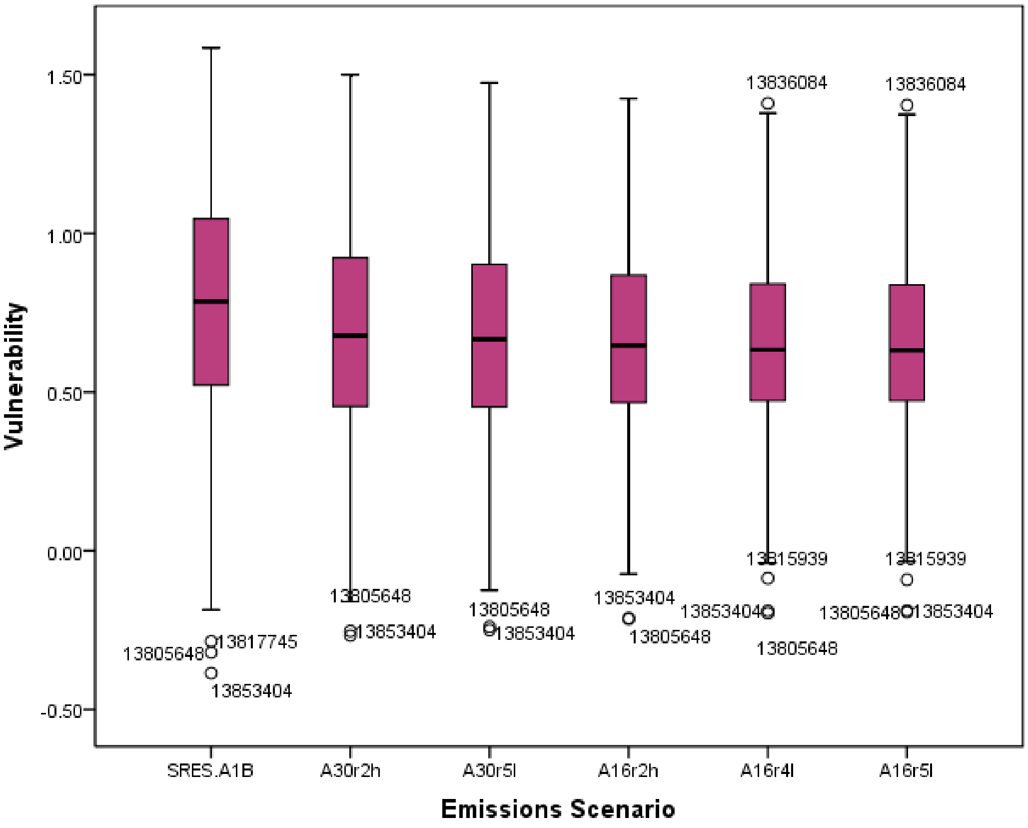
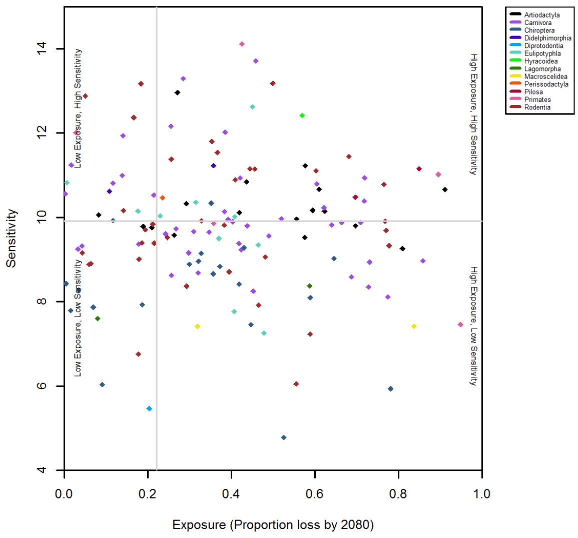
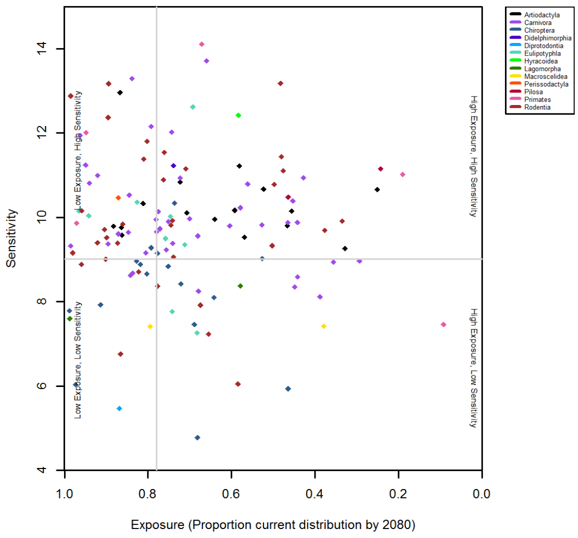


Figure 5.5 Vulnerability by Emissions Scenario (Scaling Least Concern (-0.39) to Extremely Vulnerable (1.58))

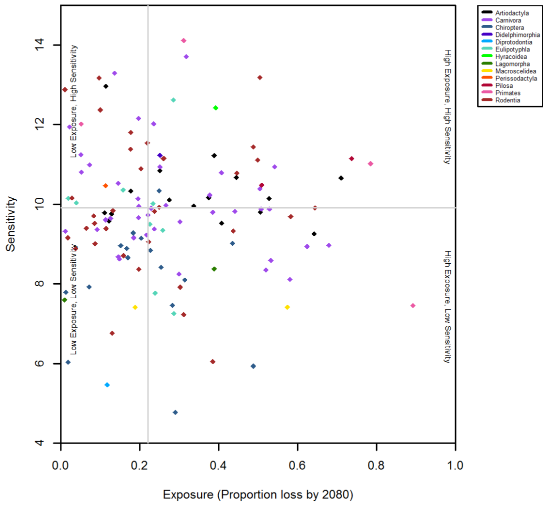
To visually explore the impact of the different emission scenarios on the overall Vulnerability of a species, plots were created for each of the scenarios (Figure 5.6 a-f). These figures and the remainder of this section on Vulnerability used the Exposure^{L}. The plots indicate the number of species occurring within each of the major classifications of Vulnerability i) Extremely Vulnerable (High Sensitivity, High Exposure), ii) Highly Vulnerable (High Sensitivity, Low Exposure), iii) Moderately Vulnerable (Low Sensitivity, High Exposure) and iv) Lowly Vulnerable (Low Sensitivity, Low Exposure). The fifth classification, Least Concern, those species expected to expand their ranges under climate change are not shown as they are of less interest to conservationists. The quadrant thresholds are determined by the Sensitivity data and Exposure based on the thresholds set out in the Wallace Initiative and in Chapter Four of this thesis.



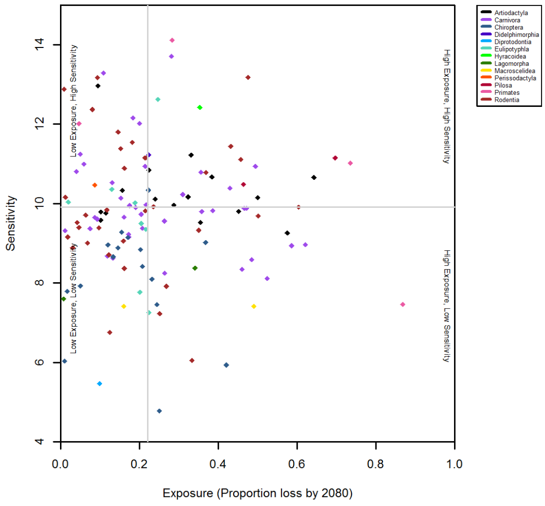
a) SRES A1B



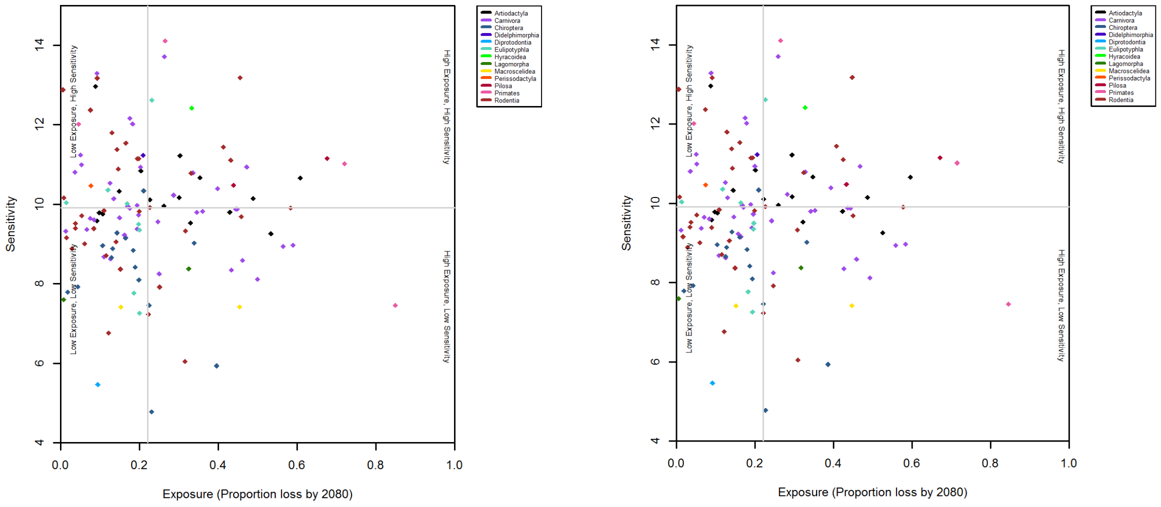
b) A30r2h



c)A30r5l



d) A16r2h



e)A16r4l f) A16r5l

Figure 5.6 Scatterplots of Vulnerability across the Emissions Scenarios (Sensitivity vs. Exposure^{L})

The scatterplots of future Vulnerability indicate the degree to which Vulnerability varies under each of the emission scenarios (Figure 5.6 a-f).

To visualise changing levels of Vulnerability across the Emission scenarios Figure 5.8 in concert with Table 5.5 examine changes in Vulnerability classifications across the species dependent on Emission scenario. Species are classified as Extremely Vulnerable if their Vulnerability score is above 1.4, representing the top 10% of scores. Species are classified as Highly Vulnerable if their Vulnerability score is between 0.9 and 1.4. Moderately Vulnerable are those species having Vulnerability scores between 0.7 and 0.9. Species with Vulnerability scores between 0.4 and 0.7 are classified as Lowly Vulnerable and those recorded to have scores below 0.4 are Least Concern.

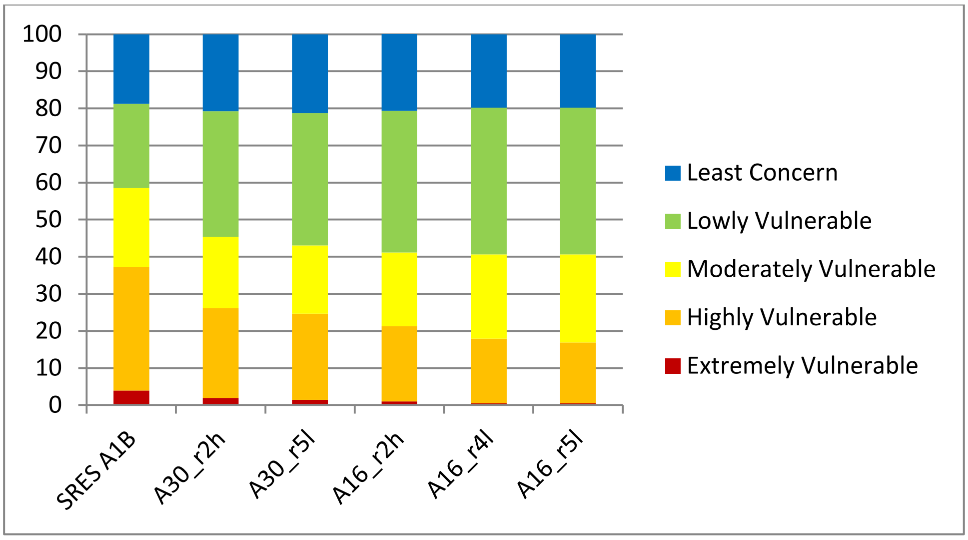


Figure 5.8 V ulnerability Classifications (Percentage species by classification in 2080)

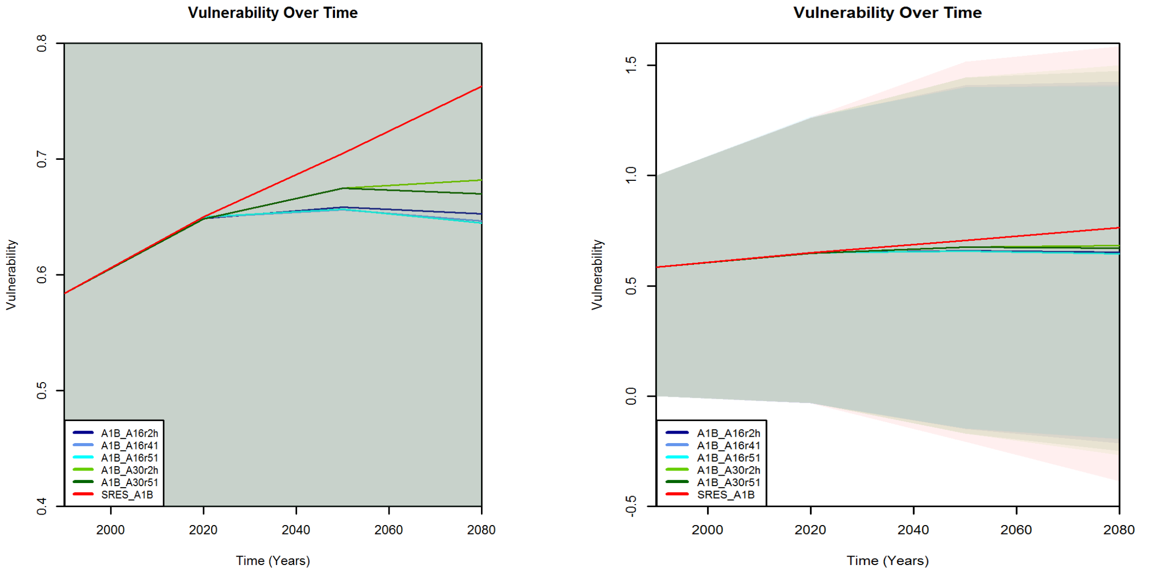
Under the business-as-usual scenario, SRES A1B, 58.5% of the total species fall into the categories Moderately to Extremely Vulnerable, with the Highly Vulnerable category contributing the largest proportion (33.3%,Table 5.5). Comparably, under the most strict mitigation scenario, A16r5l, 40.6% of species are predicted to be Vulnerable with 1 species classified as extremely vulnerable. Early and strict mitigation prevents a further 17.9% of the total species from becoming Extremely Vulnerable which would otherwise have been classified as such under the business-as-usual, SRES A1B scenario. For all scenarios, except the SRES A1B, the majority of species are predicted to fall into the Lowly and Least Vulnerable categories, with 54.6% (A30r2h) to 59.4% (A16r5l) in this classification.

Mitigation Scenario		**Vulnerability Classification at 2080**(% Total Species)				
Level	**ES**	**Extremely Vulnerable**	**Highly Vulnerable**	**Moderately Vulnerable**	**Lowly Vulnerable**	**Least Concern**
None	SRES A1B	3.9	33.3	21.3	22.7	18.8
Moderate	A30r2h	1.9	24.2	19.3	33.8	20.8
	A30r5l	1.4	23.2	18.4	35.7	21.3
Strict	A16r2h	0.5	20.3	19.8	38.2	20.8
	A16r4l	0.5	17.4	22.7	39.6	19.8
	A16r5l	0.5	16.4	23.7	39.6	19.8

Table 5.5 Vulnerability Classification by Mitigation Scenario

Exploring Changing Vulnerability through time

Plots of Vulnerability were created to examine trends in Vulnerability over the period 1990 to 2080(Figure 5.9a,b).



a) Average Vulnerability over time (zoomed)

b) Average Vulnerability over time showing full variation around the mean

Figure 5.9 Average Vulnerability of species over time by Emission Scenario (1990-2080)

The degree to which species vary in Vulnerability across the emission scenarios is illustrated by the shaded polygons which detail minimum and maximum scores of Vulnerability across the time periods. Figure 5.9a provides a close up Average Vulnerability across the emission scenarios whereas Figure 5.9b illustrates the full degree of variance in Vulnerability scores across the period 1990-2080. The largest Vulnerability scores are attributed to the SRES A1B scenario ranging from 1.26 at 2020 and increasing linearly to 1.58 at 2080. The lowest values of Vulnerability at 2050 and 2080 are also realised under the SRES A1B scenario, at -0.22 down to -0.38, respectively.

In order to bringer greater clarity to this analysis of trends in changing Vulnerability over time and to compare the impact of implementing mitigation with no mitigation average values of Vulnerability under each mitigation scenario for each time period are shown in Table 5.6.

	Average Vulnerability Score by Time Period		
Level of Mitigation	**2020**	**2050**	**2080**
Strict	0.65	0.65	0.65
Moderate	0.65	0.67	0,67
None	0.65	0.70	0.76

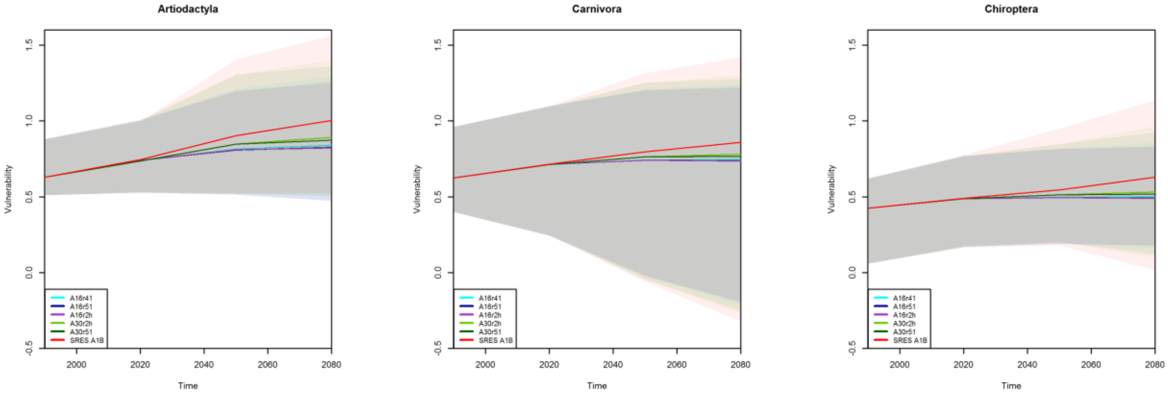
Table 5.6 Average Vulnerability over Time by Mitigation Level

The period 1990-2020 is that of greatest change in Vulnerability with an increase of 0.06 across the full suite of emission scenarios. This period of increasing Vulnerability reflects the locked-in warming predicted to occur in the early part of the 21st century due to past emissions (Fischlin *et al.* 2007).

During the period 2020-2050 the impact of mitigation policy is beginning to become apparent with a 2 point variation in Vulnerability between the A16 and A30 scenarios and a 5 point variation between the A16 and SRES A1B scenarios. In 2080 the variation across the mitigation scenarios is more pronounced represent an 11 point decrease in Vulnerability where strict mitigation is implemented during the period 2050-2080.

Beyond 2020 vulnerability changes very little across the A16 scenarios, with on average ±1 point difference between 2020 and 2080. The A30 scenario' predictions diverge at 2050 with a 2 point difference in Vulnerability at 2080 (A30r5l Vulnerability=0.66, A30r2h Vulnerability=0.68).

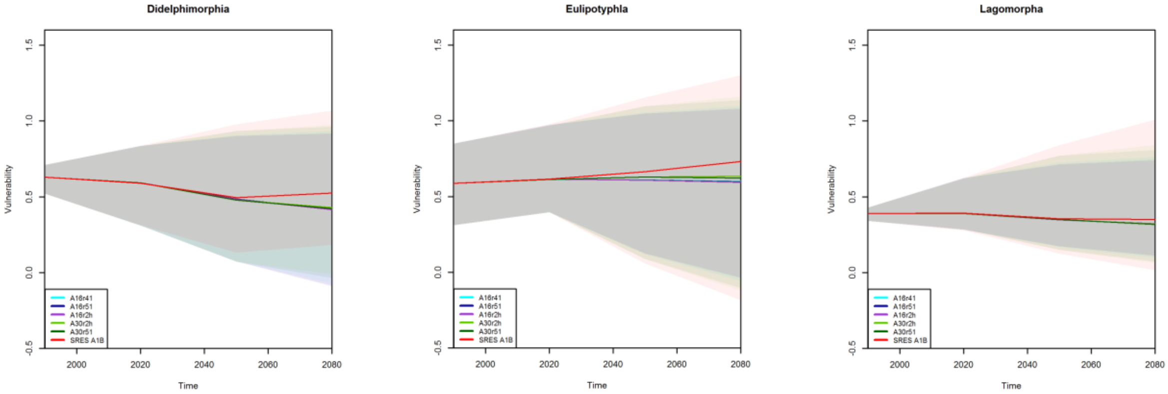
Vulnerability by Order over time



a) Artiodactyla

b) Carnivora

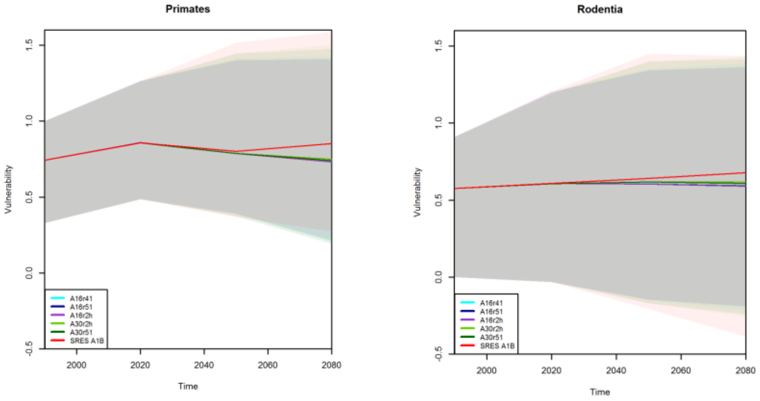
c) Chiroptera



d) Didelmorphia

e) Eulipotyphla

f) Lagomorpha



g) Primates

h) Rodentia

Figure 5.10 Vulnerability 1990-2080 illustrating the changing levels of Vulnerability between the period 1990 to 2080 by Order under the suite of emission scenarios

The four Orders with the lowest mean Vulnerability (Figure 5.10) at 1990 are the Lagomorpha (Vulnerability=0.39), the Chiroptera (Vulnerability=0.42), the Rodentia

(Vulnerability=0.57) and the Eulipotyphla (Vulnerability=0.58). The Primates are the Order with the highest mean Vulnerability scored at 0.744 in 1990.

		Time Period (% change in Vulnerability)			**Total Percentage change** (+/-)
Order	**Emission Scenario**	**1990-2020**	**2020-2050**	**2050-2080**	**1990-2080**
Artiodactyla	Strict	+11.0	+6.9	+1.6	+19.5
	Moderate	+11.0	+11.0	+3.5	+25.5
	None	+11.5	+15.7	+11.3	+38.5
Carnivora	Strict	+9.0	+2.0	0.0	+11.0
	Moderate	+8.8	+5.1	+2.3	+16.2
	None	+9.0	+8.3	+6.2	+23.5
Chiroptera	Strict	+6.3	0.0	0.0	+6.3
	Moderate	+6.2	+2.5	0.0	+8.7
	None	+6.3	+5.6	+8.4	+17.2
Didelmorphia	Strict	-3.9	-10.7	-6.7	-20.4
	Moderate	-3.8	-11.3	-5.5	-20.6
	None	-3.0	-9.6	+3.0	-9.6
Eulipotyphla	Strict	+2.7	0.0	-1.0	+1.7
	Moderate	+2.6	+1.0	0.0	+3.6
	None	+2.9	+7.6	+11.8	+22.3
Lagomorpha	Strict	0.0	-4.2	-2.6	-6.8
	Moderate	0.0	-4.1	-3.0	-7.1
	None	0.0	-3.4	-4.0	-7.4
Primates	Strict	+11.3	-7.0	-5.4	-1.1
	Moderate	+11.2	-6.8	-4.7	-0.3
	None	+11.2	-5.5	+5.1	+10.8
Rodentia	Strict	+3.3	-3.5	-1.5	-1.7
	Moderate	+3.2	+1.0	0.0	+4.2
	None	+3.2	+3.2	+3.7	+10.1

Table 5.7 Trends in average Vulnerability over time by Order (Per cent changes, increased Vulnerability indicated by '+' and decreasing Vulnerability by '-')

The maximum Vulnerability score is attained under the SRES A1B scenario by a species of Primate with a maximum value of 1.58 at 2080. The Primates consistently contain the species with the greatest Vulnerability under all emission scenarios during all periods (Vulnerability =1.0 (1990) to 1.58 (SRES A1B 2080)). The Order which consistently holds the species with the lowest Vulnerability score is the Rodentia, ranging between -0.033 at 2020 under the full suite of scenarios to -0.380 under the SRES A1B scenario at 2080.

During the 2020s Vulnerability scores are fairly consistent across the emissions scenarios, with no significant difference being discerned when accounting for the differences across Orders (One-way ANOVA *F (*5, 1236) =0.006, *p*=1.0)(Table 5.7). Similarly, an ANOVA performed across the emission scenarios at 2050 also reported non-significance ((*F*=5, 1236) =1.786, *p*=0.113). However, by 2080 the variation across the Emission scenarios is more marked between the Orders with an ANOVA returning a result indicating a significant difference in Vulnerability across the emission scenarios (*F*=5, 1236) =11.40, *p*=0.000).

The instigation of strict mitigation causes Vulnerability to reduce or stabilise between 2050 and 2080 from its peak at 2020 for all Orders the only exception being the Artiodactyla for which Vulnerability continues to rise (Table 5.7). Strict mitigation has the effect of halving, or more, the predicted increase in Vulnerability projected under the business-as-usual no mitigation scenario by 2080. This effect is particularly apparent for the Eulipotyphla where the increase in Vulnerability falls from 22.3% to 1.7%. Under strict mitigation the increased Vulnerability predicted between 1990-2020 is all but reversed by 2080 for both the Primates and the Rodentia resulting in a slight decrease in overall Vulnerability across the two Orders compared to 1990. Moderate mitigation is observed reducing or stabilising Vulnerability levels at 2080 for all Orders but the Carnivora and the Artiodactyla. Moderate mitigation serves to reduce overall Vulnerability across the Orders by at least a third (Artiodactyla and Carnivora) over no mitigation. Two Orders the Didelmorphia and the Lagomorpha are predicted to experience a decrease in Vulnerability over the period under all three levels of mitigation. It is important to remember that these are average trends and there is wider variation around the mean values for all Orders (Figure 5.9a-h).

5.3.3 The Impact of Mitigation on Spatial Patterns of Vulnerability

As discussed in Chapter Four there is inherent variability in the degree to which different sites and regions have and are predicted to experience exposure to climate change, in the magnitude, duration and the frequency of periods of favourable and unfavourable climates (Jackson *et al.* 2009).

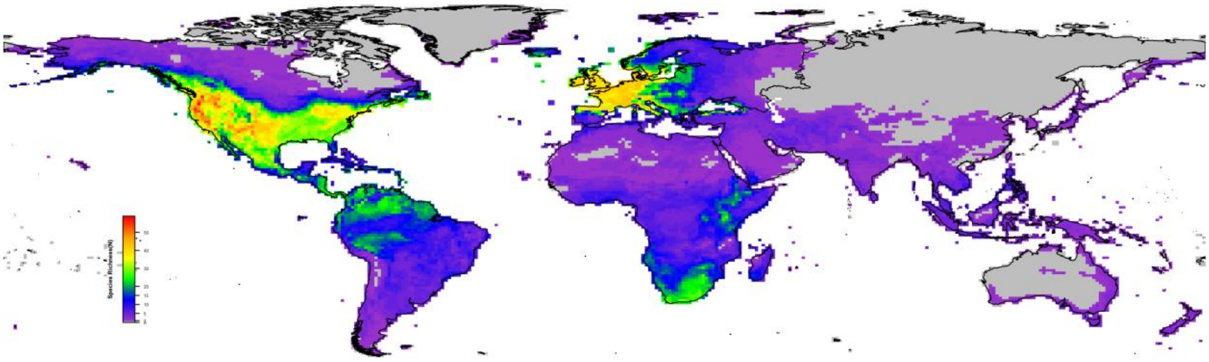


Figure 5.11 Species Richness Map (LHTd213)

In the previous chapter it was recognised that impacts of future climate change are not geographically uniform. Under the SRES A1B scenario the regions in which species are found to be most Vulnerable are the Neotropical, Afrotropical, Palearctic and northern latitudes of the Nearctic zone. In order to examine whether this same spatial pattern would exist under mitigation scenarios a series of maps were created (Figure 5.12) illustrating Vulnerability (% most vulnerable) globally. To calculate percent Most Vulnerable, the number of species in each grid cell was summed. A map of species richness (Figure 5.11) is included so that comparison can be made between Vulnerability and species richness in the database within the particular zone.

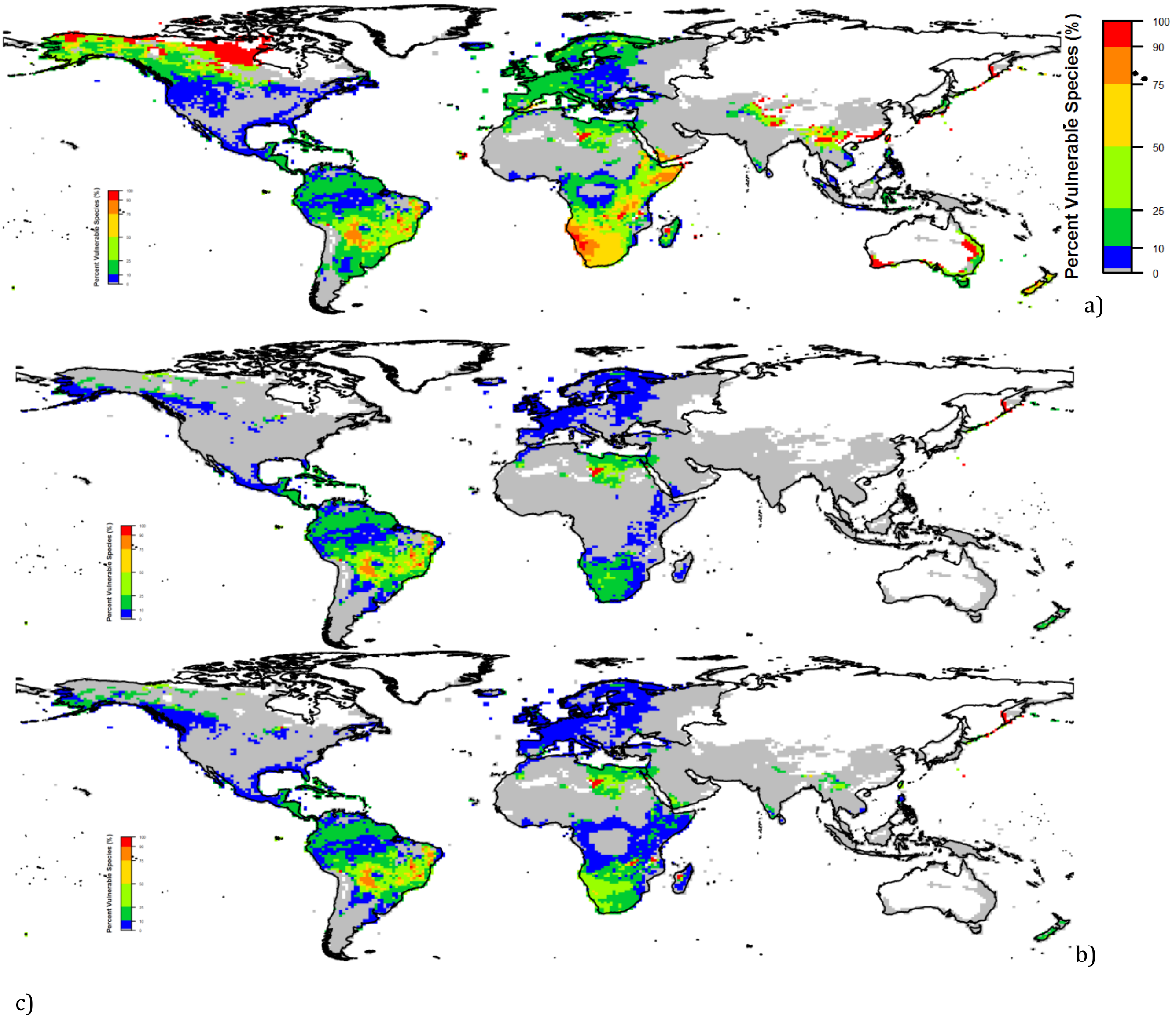


Figure 5.12 Vulnerability Maps a) SRES A1B, b) A16r5l, c) A30r5l (Percentage Most Exposed %)

The stringent mitigation scenario (A16r5l) significantly reduces the level to which the Afrotropical zone, the Palearctic and the northern latitudes of the Nearctic zone are impacted, both in terms of the extent of the region affected and also with regard to the percentage of species remaining among the most Vulnerable. Across the Palearctic zone the percentage of Most Vulnerable species reduces from 25% to 10% with the area over which species are Vulnerable greatly reduced. The impact of mitigation in the northern latitudes of the Nearctic is to virtually eliminate risk to species in this region with a very much reduced area in which vulnerable species are predicted to occur. In addition to this the number of ‘at risk’ species falls to below 10% from 25-50% under the business-as-usual scenario. In the Afrotropical zone a similar trend is observed with the highlighted ‘hotspot’ in which the most vulnerable species occur being much reduced, from extending across the major part of sub-Saharan Africa to being restricted to the Southern states only. Within this Southern region the percentage of species classified as most Vulnerable reduces from between 50-75% (reaching 90-100% in some parts) to below 25%. However, benefits of mitigation in the Neotropical zone are not so strong with very little observable difference between vulnerability under the business-as-usual and stringent mitigation scenarios.

Under the less stringent mitigation scenario (A30r5l) the benefits of mitigation are smaller, but still visible. Reduction of Vulnerability in the Palearctic and Nearctic zones remains particularly strong displaying a similar pattern to that projected under the most stringent A16r5l scenario. However, across the Afrotropical zone the reduction of Vulnerability is lessened with a larger area over which species are still classified Most Vulnerable.

Species are not well-represented for the Oriental, Saharo-Arabian and Australian zones in this analysis of Vulnerability making the drawing of any conclusions about the impact of mitigation on these regions ill-conceived. However, when accounting solely for the impact of exposure across the 5351 species of the Wallace Initiative, Warren *et al* (2013) found that benefits from mitigation were particularly strong for both, Australia and Central Asia. Due to the lack of species represented in these regions the degree to which they harbour sensitive species cannot be determined from this analysis. If Exposure is discovered to be the main determinant of mammal Vulnerability in these regions then it is likely that mitigation will strongly reduce overall Vulnerability. If, however, Sensitivity is the major determinant of Vulnerability then mitigation will play a lesser role in reducing Vulnerability.

Warren *et al* (2013) found that mitigation played a major role in reducing the impacts of exposure in the Neotropical zone, in particular within the Amazonas region. However, in the visualisation of Vulnerability, accounting for both Exposure and Sensitivity, the percentage of Most Vulnerable species is observed to remain high in the Neotropical zone even under stringent mitigation. Under the business-as-usual scenario 44% of Species are classified as Vulnerable, with 26.4% classified as Most Vulnerable. Under stringent mitigation the percentage of species classified as Vulnerable is 38.2% and Most Vulnerable remains at 26.4%. This difference in results lies in the fact that Warren *et al* (2013) concentrated solely on climate change exposure and did not account for the degree to which species are sensitive. This result implies that high Vulnerability, in this case, must be driven by Sensitivity and not by Exposure. This is confirmed by results in Chapter Three where the Neotropical zone was identified as harbouring a large proportion of Most Sensitive species, 70% of species are identified as Most Sensitive, with 54% of these being classified within the Extremely Sensitive classification. This explains why under stringent mitigation Vulnerability remains high because Vulnerability in this region is driven by Sensitivity and therefore even a small amount of climate warming is detrimental to these Most Sensitive species.

5.3.4 **Exploring GCM Uncertainty**

The Impact of Uncertainty in GCMs on projections of Exposure and Vulnerability

To illustrate the potential effect of GCM uncertainty on the Exposure and subsequently the Vulnerability measure Figure 5.13 and Figure 5.14were created for the Primates to draw attention to the similarities and differences in Exposure^R and Vulnerability predictions over time under each of the GCMs. The Primates were chosen to illustrate uncertainty because they all occur within the Neotropical zone, a region which is associated with large GCM uncertainty (Appendix Three: Visualising Climate Change.) The mean projection under each GCM is shown with variation across the species predictions shown by the shaded polygons. The seven GCMs are the UKMO-HadCM3 (UKMO3), CCCMA-CGCM3.1, (CCMA) IPSL-CM4 (IPSL), MPI-ECHAM5 (MPI), UKMO-HadGEM1 (UKMO1), CSIRO-Mk3.0 (CSIRO), and NCAR-CCSM3.0 (NCAR). The clipped mean of the five GCMs in greatest agreement is also shown as a purple line. A wider discussion of uncertainty associated with GCMs is included in Appendix Three: Visualising Climate Change. As discussed in further detail in Chapter Four uncertainty between GCMs relates to the method and mechanisms by which different aspects of the Earth system is represented within the model (Buisson *et al.* 2010).

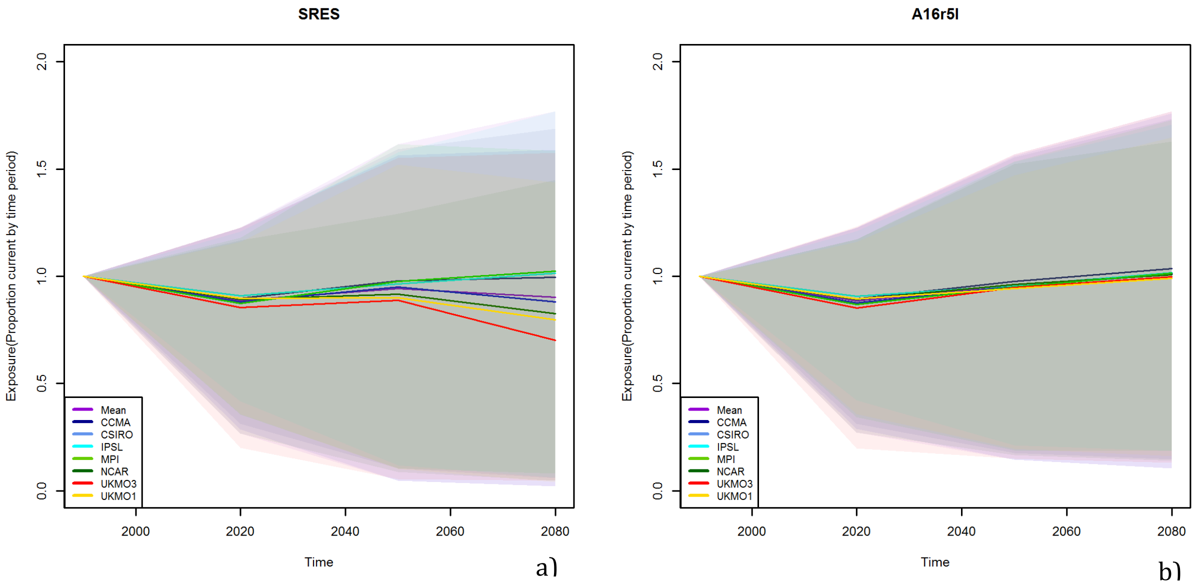


Figure 5.13Impact of GCM Uncertainty on Projections of Future Exposure^R (Primates) a) SRES A1B, b) A16r5l

Uncertainty under the SRES scenario is broad with the two outlying simulations in the SRES A1B ensemble being the UKMO3 and the IPSL. The differences in projections are equivalent to a 25% reduction under the UKM03 at 2080 compared to stabilisation under the IPSL. GCM uncertainty within the A16r5l is very narrow with no outliers, thus, one can have more confidence in the prediction of future distributions formed by taking the mean. These differences in uncertainty across the two emissions scenarios may be rooted in the interpretation of the emission scenario by the GCM. Emissions outcomes for any one storyline can vary markedly due to the interpretation of the storyline relating to differences between the GCMs in the way that they quantify socio-economic assumptions (New and Hulme 2000). Individual modellers will have been obliged to make subjective judgements in defining the storylines regarding the structure of their model and the parameter values input into the model (New and Hulme 2000). Climate projections for the SRES scenario were already available from CIAS from each of the GCMs (Warren *et al* 2013). Whereas, the GCMs had not been run previously for the AVOID scenarios (Warren *et al* 2013) therefore one would assume that when the Wallace Initiative undertook to run the scenarios the initial conditions entered would have been the same across the GCMs. This explains why uncertainty surrounding the mean SRES projections is appreciably broader than the very limited degree surrounding the A16r5l projections.

Across the Primates, their environmental niche requirements are heavily driven by temperature variables (unpublished data, Warren *et al* 2013). In Appendix Three: Visualising Climate Change, the UKMO3 was identified as being particularly 'hot', thus driving contraction in species climate space. Whereas, the IPSL was identified as representing a 'cool' simulation, explaining why suitable climate space appears to stabilise under this GCM. The mean calculation of future Exposure^R, equates to a 10% reduction in future suitable climate space, edging slightly towards the cooler simulation of future climate change.

Impact of GCM Uncertainty on Vulnerability

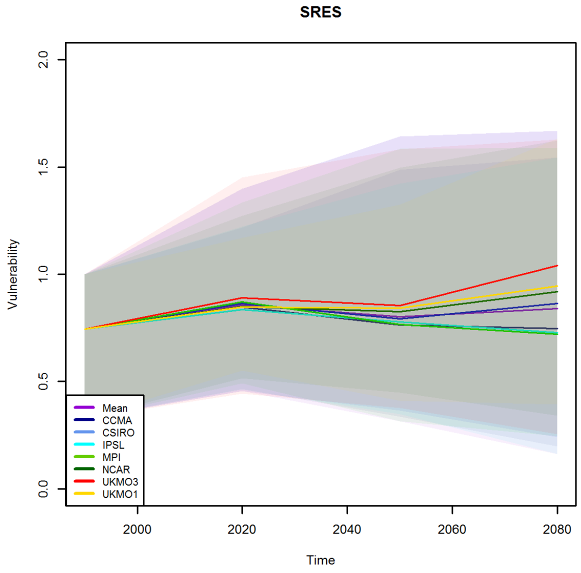


Figure 5.14 Uncertainty in Vulnerability Projections aross the GCMs (Primates)

Uncertainty across the Vulnerability projections is understandably directly relatable to uncertainty associated with the exposure calculation with the seven GCMs lining up in the same pattern as under the Exposure^R calculation (Figure 5.17). Vulnerability is greater under the UKMO3 and least under the IPSL as would be expected.

The creation of ensemble projections is widely recommended as a tool to reduce uncertainty whilst also aiding a better understanding of the breadth of uncertainty across the climate projections (Beaumont *et al.* 2008; Buisson *et al.* 2010; Jones *et al.* 2013). This process of running an ensemble model allows us to account for a range of potential climate futures and by the combination of the GCM projections provides a single climate future with the greatest likelihood (Buisson *et al.* 2010). As discussed in Chapter Four the Wallace Initiative takes an ensemble approach combining the projections of the individual GCMs into a single prediction of the species distribution.

5.3.5 **Impact of Dispersal on Exposure Projections**

The Wallace Initiative projections, and consequently the projections used in this analysis have an included dispersal mechanism- this represents an annual dispersal capacity of 1.5km/yr for the Mammals (Warren *et al.* 2013). Dispersal mechanisms are rarely included in the projection of future species' suitable climate space and its inclusion across such a large number of species, as in the Wallace Initiative, had not previously been achieved. The capacity of species to disperse to new suitable climate space is theorized to be very important in ensuring species are able to track suitable climate space (Zurell *et al.* 2009). This section investigates the extent to which manipulation of dispersal rate influences projections of future impacts of climate change. The Primates are used as an example Figure because a degree of recovery is indicated in the projections which required further investigation as to whether it is a consequence of the dispersal mechanism. Thus, projections under a realistic dispersal scenario, based on the literature concerning mammal dispersal capacity as detailed by Warren *et al.* (2013), and under a scenario representing no dispersal are compared.

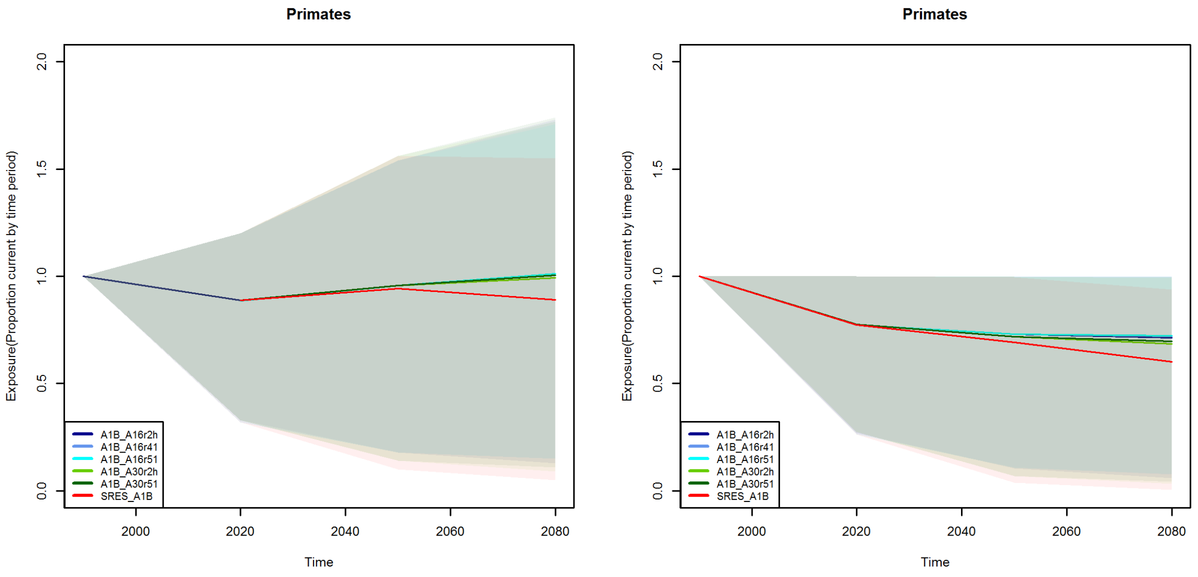


Figure 5.15 Projections of the impact of future climate change on Primates under the Emissions Scenarios to 2080 a) Real dispersal (5km/yr) b) No dispersal

Under the scenario in which dispersal is included (Figure 5.15a), the Primates are projected to experience a mean loss in suitable climate space of 10% at 2080 under the SRES A1B scenario. The equivalent scenario under a no dispersal scenario suggests that Primates will experience an average loss of 43% by2080 under the SRES A1B scenario. Without the capacity to disperse Primates are predicted to experience an average contraction of 33% above that of the dispersal scenario indicating that the capacity for dispersal strongly influences species ability to track suitable climate space.

Further of interest is whether the recovery predicted between the years 2050 to 2080 is related to dispersal capacity or whether it is apparent under the no dispersal as well. Under the no dispersal scenario after an initial decline to 2020, post-2020 the mitigation scenarios suggest that recovery to former parts of the distributions is not expected. This indicates that dispersal is playing a key role maintaining the species range extent by tracking suitable climate space.

It is important to recognise that this mechanism of dispersal cannot take into account habitat connectivity which is identified as important in facilitating or hampering species' ability to track future climate space (Graham *et al.* 2010; Jaeschke *et al.* 2012).

5.4 Discussion

This chapter has analysed projected climate change under a suite of emissions scenarios and how variation in each affects species Exposure and subsequently Vulnerability. It has sought to allow conclusions to be drawn upon the impact of mitigation in avoiding the worse predicted impacts of climate change upon biodiversity. The production of projected Exposure and Vulnerability over time means we are better able to pinpoint the time period in which mammal species are most vulnerable.

5.4.1 **What effect does mitigation have on overall species Vulnerability?**

Mitigation scenarios are recommended for the investigation of different policy approaches on species distributions with comparisons between different emissions scenarios commonly addressed (Thuiller 2004; Barbet-Massin *et al.* 2009; Lawler 2009). However, examples of this approach to assess taxonomic trends are rare (Foden *et al.* 2013; Warren *et al.* 2013). This makes drawing comparisons between this analysis and other approaches difficult.

The Impact of Mitigation on levels of Overall Vulnerability

Mitigation serves to reduce the percentage of species classified as Moderately Vulnerable or higher from 58% to 40.6% under strict mitigation, a factor of 1.44. This reduction in overall Vulnerability is clearly linked to changing Exposure because the Sensitivity component of Vulnerability is fixed. Foden *et al* (2013), in an assessment of climate Vulnerability for the birds and amphibians investigated three SRES emissions scenarios for two time slots 2050 and 2090, these scenarios are ‘B1’ representing low range climate change, ‘A1B’ moderate range change and ‘A2’ high range climate change. They predicted that under the low range scenario overall vulnerability would fall by a factor of 1.25 for amphibians and 1.42 for birds compared to under moderate warming at 2090, the no mitigation scenario in this analysis. Mitigation serves to reduce overall Vulnerability for all Orders examined, and in some the case of the Primates serves to entirely reverse the impact of locked-in warming predicted to impact in the early part of the 21st century.

How does Mitigation affect Vulnerability over Time?

In the previous section the potential benefits of mitigation were found to relate to the timing of its implementation, with early mitigation (strict mitigation 'A16r5l') reducing future exposure to a larger extent than delayed mitigation (moderate mitigation 'A30r5l'). To see whether this is the case in terms of reducing overall Vulnerability the mitigation scenarios are compared with relation to time. Several studies have investigated the impact of different mitigation scenarios over time (Wigley *et al.* 1996; Yohe and Strzepek 2007). However, few studies have sought directly to compare the impacts of different scenarios of mitigation on species survivorship (Foden *et al.* 2013; Warren *et al.* 2013).

Due to the effect of locked in warming predicted to occur over the decades to 2020 (IPCC 2007) Vulnerability is observed to remain fairly constant across the emission scenarios. This effect of locked-in warming was also observed by Buisson *et al* (2010) who found that the emissions scenario employed counted for very little variation between projections of future climate change during this period, however, they did find that variation between different scenarios increased as the time horizon increased. A finding further evidenced in this study as beyond 2020 the benefits of individual mitigation scenarios begin to accumulate. At 2050 the strict mitigation scenarios reduce average Vulnerability from 0.70 under the business-as-usual scenario to 0.65, a reduction in potential Vulnerability of 8%. Under the moderate mitigation scenarios, this reduction in Vulnerability is narrowed to 5%. The potential reduction in impacts gained by mitigating early is thus a further 3% above that achieved by implementing mitigation later.

At 2080, the potential avoided impacts by mitigating early are further apparent, at 2080 the strict emissions scenarios reduce average Vulnerability from 0.76 under the business-as-usual scenario by 0.64, equivalent to an average reduction of 15% of an individual's Vulnerability. Under the moderate scenarios, this is narrowed to an average 12% decrease in individual species Vulnerability. The potential reduction in impacts gained by mitigating early is narrowed slightly, equivalent to 4% above that achieved by implementing mitigation later.

Foden *et al* (2013) found that the percentage of species assessed as having high climate change vulnerability remained fairly similar to 2050 across the high, moderate and low scenarios they analysed. This is at odds with the results of this analysis which suggest that with early mitigation Vulnerability is lower than that of no mitigation (equivalent to the moderate scenario of Foden *et al* (2013). This deviation relates to the difference in scenarios used to analyse future levels of climate change, the B1 scenario Foden *et al*. (2013) employ to represent 'low range climate change' represents a less aggressive mitigation pathway to that represented in the strict mitigation (A16) used here lying between this analyses strict and moderate mitigation scenarios (Arnell and Lloyd-Hughes 2013). However, they found that estimates of Vulnerability began to diverge across the three scenarios to 2090 by a factor of 1.42 for birds and 1.25 for the amphibians. As discussed earlier in this discussion this trend mirrors that found in this analysis with the impact of early strict mitigation become increasingly apparent to 2080. This highlights even more clearly the potential benefit of mitigation for a broad swathe of taxa, particularly the further benefit of early mitigation in avoiding the worse potential impacts of climate change.

The Impact of Mitigation on Spatial Patterns of Vulnerability

The implementation of strict Mitigation was found to reduce overall Vulnerability, significantly reducing vulnerability in the Afrotropical, Palearctic and Nearctic zones. Vulnerability remained high in the Neotropical zone with strict mitigation providing little benefit. Foden *et al* (2013) also examined patterns of changing Vulnerability across the three scenarios they investigated; the most salient for comparison here are the low and moderate climate scenarios. Foden *et al* (2013) report a reduction in overall vulnerability for the Afrotropical zone, specifically the Congo basin, for the Birds and the Neotropical zone, around the Amazonas, for Birds and Amphibians. Vulnerability remains fairly constant across the remaining zones with low levels of Vulnerability across both scenarios. The most striking difference between these two assessments of spatial vulnerability is centred on the Neotropical zone, with Foden *et al* predicting total number of vulnerable species to fall from between 326-390 to between

1-65 for birds and from 28-40 to 0 for Amphibians under the low mitigation scenario. There are several possible explanations for this difference, the most likely source being, i) the difference between Foden *et al's* (2013) low mitigation scenario and the strict mitigation scenario used here, and ii) taxon-specific levels of sensitivity, iii) Vulnerability classification thresholds. High sensitivity in the Neotropical region across the mammals examined in this study (Chapter Four) is likely to be linked to Vulnerability remaining high even under the strict mitigation scenario.

5.4.2 The limits of Mitigation: Are there species for which Mitigation has no impact on the degree to which they are Vulnerable?

There is a single species for which mitigation has no impact on its Vulnerability, and which remains classified as Extremely Vulnerable under the strictest mitigation, this is the Brown-mantled tamarin (*Saguinus fuscicollis*). Although mitigation does serve to lessen the degree to which it is predicted to be Vulnerable by up to 12% under the strict mitigation scenario. The fact that the Brown-mantled tamarin remains Vulnerable under mitigation is related to its high Sensitivity score which puts it in the upper quartile of scores (Sensitivity=11.08). This in combination with the projected loss of 71% of its current climate space under even the most stringent mitigation scenario places it beyond mitigation help. Foden *et al* (2013) provide no evidence relating to individual species remaining highly vulnerable under their low climate scenario (SRES B1).

5.4.3 Justification of methods and Caveats

Mitigation Scenarios and Model Uncertainty

Beaumont *et al* (2008) state that in order for policymakers and environmental managers to make decisions about mitigation or conservation strategies on the basis of model-based assessment of the impacts of future climate change on species information they must be provided with information regarding the potential uncertainties inherent in the analysis. This includes providing information on a) the climate models used, b) the emission scenarios used and reasons for their selection, c) features of the climate model realisation, and d) downscaling techniques. In this chapter the criteria concerning choice of emissions scenarios and reasons for selection is the most relevant, a synopsis of the other criteria is available in Chapter Four but see Warren *et al* 2013 for in depth information.

Selecting the Emission Scenarios

The uncertainty relating to spatial and temporal uncertainty surrounding the degree of climate change impacts poses a substantial challenge for policy makers and environmental managers alike. Identifying the uncertainties relating to these projections therefore is important. By testing a range of different mitigation scenarios, as in this study, we are better able to assess the types of species responses possible under different policy decisions aimed at reducing emissions (Beaumont *et al* 2008, Buisson *et al* 2010; *Warren et al* 2013). Selecting a range of mitigation scenarios which encompass conservative, moderate and optimistic levels of emissions reductions allows impacts modellers to explore the breadth of possible influence of different policy strategies in shaping the level of climate change projected to occur (Beaumont *et al* 2008). This analysis takes into account six emissions scenarios, one business-as-usual scenario, two moderate scenarios, described as such because emissions peak is set at 2030, and three optimistic scenarios, with emissions peaking in 2016.

One component of uncertainty in species distribution models is that introduced by future climate scenarios (Beaumont *et al* 2008; Buisson *et al* 2010, Dormann 2008). Climate scenarios are constructed to represent alternative plausible future climates. There are two forms; idealized scenarios which determine *a priori* change in climatic variables, and those scenarios derived from integrating climate models with projections of greenhouse gases (Beaumont *et al* 2008). Idealized scenarios imply a homogenous change in the climate variables across the study region and do not allow the species response to temporal change to be estimated. The Wallace Initiative avoids introducing undue restrictions and therefore inflated uncertainty in this way by using the infinitely more robust method and employing projections from a climate model (Warren *et al* 2013).

Reducing internal sources of Uncertainty to reveal impact of Mitigation

In their paper aimed at quantifying the uncertainty contribution of individual components of species distribution models Dormann *et al* (2008) found that model type and data quality were the major contributors with variation in scenarios accounting for very little. However, this result is caveated by the fact the study region was narrow and accounted for a relatively small range of climatic conditions. Buisson *et al.* 2010 further scrutinized sources of uncertainty in species distribution models examining the impact of emissions scenarios alongside that of GCMs, initial data and model choice. Buisson *et al* (2010) chose to compare four alternative SRES scenarios A1F1 (most pessimistic), A2, B2 (intermediate), B1 (most moderate) chosen to encompass a range of greenhouse gas emissions projected for the 21st century. They found that SDM choice was the major contributor followed by GCM, whose contribution increased over time to a point where the proportion of variance GCM explained almost equalled that of SDM. Comparatively initial data and emissions scenario contributed little to explain the overall variance, explaining around 10% of overall variance. However, over time the degree of variance accountable to the emissions scenarios increased as the storylines diverged towards the end of the 21st century. This variation among scenarios is clearly understandable and divergence to be expected because the raison d'être for running alternative emission scenarios in long-term projections is to account for a sufficient sample of uncertainty in future conditions (Beaumont *et al* 2008; Meehl *et al.* 2007). As previously described in Chapter Four, the model used in this study seeks to reduce GCM uncertainty by running an ensemble model combining seven GCMS. This reduces this source of uncertainty and serves to increase the likelihood of variation observed in Exposure and Vulnerability calculations is related to the individual mitigation implemented.

5.4.4 Conclusions

This analysis illustrates the benefit of stringent early mitigation in avoiding the potential impacts of climate change on species' Vulnerability, buying time not only for species to respond to a changing climate but also for the implementation of conservation policy to aid this. It has also provided evidence as to the species and regions which remain most vulnerable even under the most stringent mitigation. This evidence is useful to the shaping of future conservation policy by identifying those most vulnerable for prioritisation. These results suggest that implementing global policies of mitigation will substantially reduce climate change vulnerability.

6 Conclusions

6.1 A Review of the Hypotheses

In order to assess the success of this research in answering those questions it sought to investigate means a return to those set out in Chapter Two. With regards to whether levels of individual species' sensitivity can be described by life history and ecological traits this study has shown that trait data can be used to infer sensitivity, and that in combination these traits can be used to describe whether species are highly or lowly sensitive to climate change. Past Exposure was shown to have a weak influence in determining patterns of sensitivity in the landscape this information therefore can be used to validate the measure of sensitivity based on traits. However, it also served to reveal the influence of other factors, biotic and abiotic, in determining current species distributions. Patterns in life history and ecological trait combinations among species can be loosely associated with the Order to which they belong. However, the strength of this association is low and wide variation across these traits among species within a single Order means that the assessment of individual species' sensitivity cannot be based solely on the Order to which it belongs. It was hypothesised that globally sensitivity levels would fluctuate as a function of past exposure filtering sensitive species and therefore regional biotas experiencing high velocities of past climate change would be less sensitive. Although no difference was determined between sensitivity levels across the Tropical and Temperate regions at the scale of biogeographic zone patterns of sensitivity were observed within zones although not entirely relatable to past climate change. This analysis was unable to robustly test the association between restricted species and sensitivity as too few records were available.

With regards to the hypotheses investigated around the measurement of vulnerability this analysis investigated both the impact of exposure alone and in combination with sensitivity through the development of a unique measure of Vulnerability. It determined the percentage of species determined as at risk under exposure only and compared this with percentage vulnerable to future climate change, finding that the number of species classified as at risk increased with the addition of information on sensitivity. This study found that species and regions identified as highly exposed under future climate change did not necessarily translate into being highly vulnerable as factor of their sensitivity and vice versa. There are Orders identified in this analysis as being more vulnerable to future climate change than others having being both highly sensitive and predicted to experience high future exposure. There are also Orders predicted to be highly exposed but have low Vulnerability overall as a function of their low sensitivity. This analysis also identified patterns in spatial Vulnerability with some regions harbouring high proportions of vulnerable species.

Mitigation was found to reduce overall exposure levels by effectively reducing the degree of warming predicted to occur. Mitigation was observed to reduce species vulnerability; however, there are some species for which mitigation has very limited impact on the degree to which they are predicted to be vulnerable. This is a result of these species' high sensitivity to even the smallest degree of warming.

The Utility of assessing Sensitivity on the basis of traits

The loose association found between individual species' sensitivities and the Order to which they belong puts into doubt the utility of using average Order Sensitivity to determine that of individual species for which we have little information. This study has identified traits which inflate species sensitivity and, therefore, species can be assessed against this sensitivity trait set using this information. However, because the Sensitivity measure developed here is relative comparison between species Sensitivity scores assessed within this analysis and in future assessments is ill-advised.

6.2 How can this Assessment support Conservation management decisions?

In order to draw conclusions as to the utility of this assessment in aiding conservation management it is first important to set the context in which conservation managers must make their decisions.

Climate change is likely to challenge the dominance of the current driving principal of conservation action, 'management for resilience' and to force conservationists to adopt management practices which allow 'management for change' (West *et al.* 2009), adaptive management. Understanding likely current and future climate change is prerequisite to undertaking any review of management adaptation strategies (West *et al.* 2009). There is broad understanding of the physical and biological principles behind climate change and the potential large scale ecological impacts on biodiversity associated with change, however, likely responses of individual species are less well understood (Conroy *et al.* 2011).

In order to identify climate-change induced stresses Geyer *et al.* (2011) examined 20 conservation sites in 7 countries structuring those stresses identified into three levels of biological diversity, i) stresses affecting individuals and populations, ii) stresses affecting biological communities and iii) stresses affecting ecosystem structure and function. This analysis examines the impact of changes in climate, specifically temperature and precipitation (average, variability and seasonality) over the long-term in order to assess the degree to which these stressors (identified by Geyer *et al.* 2011) will impact climatically suitable space at the species level.

Conservation organizations and natural resource management groups require guidance on which to base their response to future climate change, understanding the potential broad impacts of future climate change is paramount in determining the course to follow from the myriad potential actions and strategies available (Conroy *et al.* 2011). Conservation managers are guided by a series of adaptation principles which encourage landscape-scale actions taking into account climatic impacts, the composition of the landscape and species' attributes (Oliver *et al.* 2012). However, there is evidence that a lack of understanding relating to how to prioritise, target, and implement conservation practice may serve to inhibit turning these principles into action (Oliver *et al.* 2012). This has led to the development of several frameworks aimed at translating these principles to guide conservation managers on the ground (West *et al.* 2009; Conroy *et al.* 2011; Cross *et al.* 2012; Oliver *et al.* 2012). These frameworks illustrate the process managers should undertake when assessing and prioritising species and ecosystems for management (Figure 6.1)

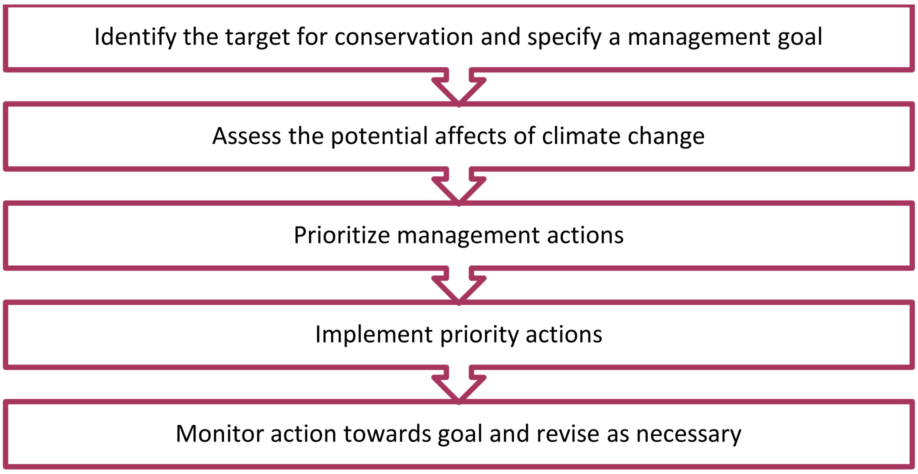


Figure 6.1 Basis Framework of Conservation Management (after Cross et al 2012)

The idea behind these frameworks is to target populations of individual species most threatened by climate change. However, the authors readily acknowledge that there is limited empirical data available on how species interact within the landscape (Oliver *et al.* 2012). Therefore, these frameworks each identify the use of modelling approaches as key to understanding the range of exposure but also identify a need for these analyses to account for sensitivity which goes beyond identifying tolerances to climatic variables.

As illustrated in Figure 6.1 understanding the potential effects of future climate change is an integral part of the process by which conservation managers prioritize management actions. Climate suitability or species distribution models form the foundation of climate change integrated conservation management (Gillson *et al.* 2013). Using information provided by distribution models, such as that developed upon in this research, aids conservation practitioners to prioritize and geographically target different actions (Oliver *et al.* 2012). Embedding plausible physical, biological and ecological responses into these models can help further direct the conservation reaction (Cross *et al.* 2012).

Past assessments of the impact of future climate change have focused on changes in spatial distribution or changing abundances, Hulme (2005) advocated the integration of aspects of species' life history and ecological preferences to better characterise the impacts of climate change to guide conservation action. Oliver *et al.* (2012) discuss the utility of using Vulnerability analysis to determine the impact of future climate change but concede that often evidence on individual sensitivities is unknown. Information on the sensitivity of individual species is key to understanding of Climate change impacts on specific conservation targets (West *et al.* 2009). These sensitivities range from aspects of individual species biology to ecological functioning of a system and along with climate change scenarios form the basis for planning under multiple possible futures (West *et al.* 2009).

This analysis has strengthened the depth of knowledge surrounding impacts of climate change on biodiversity. In brief this analysis has identified those Mammals species most vulnerable under future climate change. It has also identified the regions in which the most vulnerable species are likely to occur, specifically identifying the Neotropical, Afrotropical and Palearctic zone as harbouring high percentages of vulnerable species.

This knowledge can be incorporated into future conservation policy, in several aspects by, 1) helping to prioritise the most vulnerable Mammal species for conservation action, 2) highlighting the regions in which the most vulnerable species occur to focus conservation action, and 3) identifying the factors which confer vulnerability allowing other species (particularly Mammals) not included in this analysis to be assessed under the Vulnerability framework for prioritisation.

Conroy *et al.* (2011) write that despite uncertainty in species and ecosystems responses conservation must proceed as it cannot wait for the untangling of these uncertainties. Therefore, management actions should be guided by multiple, plausible hypotheses which undertake to describe a wide range of alternative scenarios of climate change and the subsequent impacts. Exploring the impact of different climate scenarios allows one to examine the potential range of responses species and ecosystems may undertake (Cross *et al.* 2012). Through the assessment of species vulnerability under a broad range of climate futures this analysis provides an indication of the degree to which different species will be impacted allowing for conservation managers to prioritise for conservation action those most at risk even under low climate warming. The investigation of changing Vulnerability over time provides conservation managers with a timescale over which to implement conservation actions in order to elude the worse impacts of future climate change.

Identification of the level to which different species are likely to be vulnerable to future climate change will support conservation managers by narrowing the number of potentially appropriate adaptive management options to select from. There are several forms of climate change adaptation actions suggested including creating a i) buffer zone around existing habitat patches to reduce edge impacts, ii) in-situ management improving habitat quality and to remove non-climate related threats, iii) restoring local habitat surrounding existing vulnerable sites, iv) translocation of species, and v) ex-situ management (Oliver *et al.* 2012). For Species identified as having limited dispersal ability, high sensitivity and at risk of losing large proportions of their current distribution translocation may prove the better management strategy over improving habitat connectivity (Hulme *et al.* 2005). The identification of highly vulnerable species guides the prioritization of these species for potential translocation and ex-situ conservation (Gillson *et al.* 2013). However, in order take these conservation decisions conservation managers require information on the impact of future climate change on species due to their individual sensitivities (Gillson *et al.* 2013). This analysis provides this information.

Barriers in the Landscape and Shifting Distributions

It is known that distribution patterns are governed by many factors, not solely climate, and that these influence patterns of distribution but also the rate at which distribution shifts occur (Heikkinen *et al.* 2006). These factors include, but are not limited to, habitat fragmentation, topography, and fire frequency (Brotons *et al.* 2004; Heikkinen *et al.* 2006). The influences of these external factors on the results of this analysis are complex. For example, for adaptive responses to be successful in responding to rapid climatic change the quality of habitat connectivity in the landscape must be good and the species must be able to keep pace with the velocity of climate change through dispersal or local adaptation (Graham *et al.* 2010; Jaeschke *et al.* 2012). Habitat fragmentation and natural barriers may thus restrict species dispersal (Wiens *et al.* 2009). These barriers are important in determining species ability to track climate change because any increase in the mean distance between natural habitats further compromises the ability of species to successfully disperse between populations and habitat patches (Parmesan *et al.* 2000). Habitat connectivity is not represented in consequence the model assumes that species can disperse effectively through the landscape. This is obviously unlikely to be the case because of the competing factors identified here. Therefore the model is likely to overstate the capacity for individual species to shift their distributions (see Chapter Four, Section 4.4.4). The addition of a topographical layer (describing elevation range and altitude above sea level) has been found to improve overall model predictions (Virkkalaa *et al.* 2010). However, representing these large-scale landscape features in species distribution models to prevent species being predicted to cross mountain ranges has not been attempted. Crooks *et al.* (2011) examined the effect of fragmentation and habitat connectivity on mammalian carnivore distributions finding that these factors strongly influenced extinction risk. Howard and Schlesinger (2013) integrated a measure of habitat connectivity into their model of 26 rare species distributions under climate change. The complexity of integrating connectivity data for a region the size of New York's Hudson Valley, as in their paper, illustrates the enormity of the challenge associated with achieving this on a global scale.

6.3 What evidence does this Assessment provide to support mitigation policy?

Examining the effectiveness of different policy actions in ameliorating the effects of climate change can inform conservation strategies (Gillson *et al.* 2013). This thesis demonstrates the benefit of early mitigation in reducing future vulnerability. The analysis also reveals the extent to which species remain vulnerable even under the most stringent mitigation.

With regards to mitigation policy, this analysis has added further weight to the argument that mitigation of climate change has the potential to protect biodiversity, and that without mitigation a large proportion of biodiversity will be at risk (Yohe and Strzepek 2007; Foden *et al.* 2013; Warren *et al.* 2013). It also advocates the earliest possible date for cutting emissions, and the implementation of mitigation policy to achieve this. This is in agreement with the findings of Warren *et al* (2013) in terms of reducing exposure and Foden *et al* (2013) with regards to reducing future vulnerability of species.

On the basis of observations into the response of ecosystems and their constituent species to recent warming van Vliet *et al* (2006) recommended that attempts be made to constrain future climate change to 1.5°C above pre-industrial levels, limited to less than an increase of 0.5°C per century. However, this analysis has shown that despite warming of above this threshold, ranging from between 2°C under strict mitigation to 4°C under with no mitigation, the percentage of mammals classified as extremely vulnerable is 0.5% rising to 3.9% respectively. Correspondingly, 16.4% are classified as highly vulnerable rising to 33.3% with no mitigation. This result suggests that many species are placed at high risk being highly or extremely Vulnerable under 4°C with significantly fewer under 2°C. Further, it is important to qualify that under strict migration 40.6% of the species analysed are classified as Moderately Vulnerable or higher and as a consequence are likely to require conservation action.

Barriers in the Decision-Making Process

Despite multiple lines of evidence as to the efficacy of mitigation in averting the worst predicted impacts of climate change, to which this analysis adds further weight, reaching consensus across nations to undertake mitigation action continues to prove difficult (Council on Foreign Relations 2013). The likelihood that peak emissions will be reached at 2016 is negligible, however by accounting for this scenario this research provides a benchmark for what could have been achieved if agreement had been reached. It therefore provides policymakers with an impetus to agree targets which provide steps to ensure peak emissions are reached and subsequently reduced before further damage to biodiversity occurs.

6.4 The Implications of these findings for established Conservation Prioritization Strategies

There are several global schemes designed to identify conservation priorities such as the IUCN Red list (IUCN 2012). These schemes inform policy on the protection of individual species, such as the CITEs on trade in endangered species, and also influence global investment strategies (Iwamura *et al.* 2013). It is important that these prioritisation schemes are assessed in their effectiveness with regards to future climate change (Iwamura *et al.* 2013).

This analysis advocates the inclusion of climate change vulnerability into assessments of individual species risk. If climate change vulnerability remains unassessed in these risk assessments, which are subsequently used to prioritize conservation actions, species that become increasingly vulnerable into the future under climate change may be overlooked. This includes species which are not currently assessed as at risk but are predicted to become increasingly vulnerable under future climate change. The IUCN has looked at incorporating climate change factors into their assessments (IUCN 2009) but these recommendations have not been adopted as yet.

It is important that the limited resources and funds available to for conservation managers are directed prudently. Currently, US$ 750 million are disbursed annually in supporting local conservation projects globally on the basis of the Biodiversity Hotspots analysis developed by Myer *et al* (2000) but this theory's applicability under climate change is untested and may ultimately prove to be ill-judged (Iwamura *et al.* 2013).

6.5 Implications of this Research regarding Representation of Mammal groups and Regions

6.5.1 **Mammal Representation**

Due to constraints within the data some mammal groups are either poorly characterised with few representatives or missing completely. This includes the emblematic 'poster child' of climate change the Polar bear (*Ursus maritimus*). Missing species also include the Marsupials which are significantly underrepresented due to lack of occurrence data for these species in GBIF (GBIF 2013) at the time of the analysis.

Assessing the Vulnerability of the Polar bear

Based on the components identified as increasing Vulnerability in this study one might conclude that the Polar bear is pre-destined to be highly if not extremely vulnerable to future climate change. Information is available on the Polar bear's life history traits in PanTHERIA (Jones *et al.* 2009) but missing from the Wallace Initiative due to its occurrence in the high latitudes of the Arctic (Warren *et al.* 2013). Like its close relative the Brown bear (*Ursus* a*rctos*), which appears among the 10% Most Sensitive species identified in this analysis, the Polar bear's life history is characterised by traits identified here as increasing sensitivity. Sexual maturity is only reached at an age of 5yrs, Polar bears have small litters (2 cubs per mating) and only mate once every 2-3 years (Jones *et al.* 2009). Gestation period is short but the cubs will remain with the mother for at least 2 years. In combination these traits would suggest that the Polar bear is highly sensitive to disturbances. With regards to exposure under a scenario of no mitigation temperatures are predicted to increase by of 2-3°C by 2080 (Appendix 3), this warming in the Arctic Circle will increase the rate of ice melt causing the ice sheet to shrink (IPCC 2013) negatively impacting species such as the Polar bear which rely on the ice sheet for their survival, (IUCN 2009). Together, these characteristics of Sensitivity and Exposure suggest that the Polar bear will be, as hypothesised, highly vulnerable to climate change.

6.5.2 **Regions**

There are several regions identified in this analysis for which there are large gaps in available occurrence data, preventing the assessment of exposure, and also gaps in the factors corresponding to sensitivity. These regions include Australia, Madagascar, Indonesia, Russia and China. Madagascar, Indonesia and Australia are regions of high global endemism (Ceballos and Ehrlich 2006). Endemic species are identified as particularly vulnerable to future climate change (Thomas 2010). Although data is unavailable for these areas of endemism one would hypothesise that inclusion of these species would inflate the overall percentage of species identified as Moderately Vulnerable or higher.

6.6 Improving the Vulnerability Measure

To assess which factors of Vulnerability are absent from this analysis requires returning to the Vulnerability framework as described by Williams *et al.* (2008). In terms of defining Sensitivity this analysis accounts for 'resilience' factors including those determined by life history and dispersal capacity, but, information on population dynamics is absent. The other component of Sensitivity, 'adaptive capacity,' encompassing genetic diversity and phenotypic plasticity, is entirely unrepresented in the measure developed here. The Exposure component is determined using species' climatic preferences and tolerances to explore the degree to changing climate will impact species distributions in space and time. This analysis excludes abiotic and biotic interactions and micro-habit and topographic buffering. This analysis also accounts for the impact of mitigation another factor identified as important in determining the future vulnerability of species. There are clear reasons for this analysis not incorporating several of the identified 'missing' factors. In relation to micro-habitat and topographic buffering, and biotic interactions these are not thought to be relevant to determining climate change impacts in global scale analysis such as this (Peterson and Dawson 2003). There is insufficient data relating to genetic and phenotypic diversity because they are exceptionally difficult to quantify (Williams *et al.* 2008) so at present incorporation of these factors at a global scale is all but impossible. One factor missing from this analysis' measure of sensitivity and which could be incorporated are aspects of population dynamics. Information on population trends, if not population sizes, are available from the IUCN Red list (IUCN 2012) and could potentially be incorporated by adopting the population-based criteria used to judge level of endangerment (IUCN 2001).

6.7 Modifying this Method to examine novel Taxa

The utility of the method developed here is that it could easily be duplicated for other taxonomic groups for which data on life history and ecological traits and future exposure to climate change is available. The Wallace Initiative (Warren *et al.* 2013) already provides exposure data for Amphibians, Reptiles and Birds. Assimilating life history data though is far from straightforward for these groups due to access and sharing of data which is often closely guarded by the individuals and institutions which have collected them. The calculation of the Exposure would remain the same as the set out in this research. However, it is likely that different components of life history and ecology are important in the determination of Sensitivity. For example, in amphibians variation in gestation length is unlikely to be relevant, due to the fact that they are egg-bearing, but the level of parental care could prove to be important. There are species, such as the Surinam toad (*Pipa pipa*) and the Darwin frog (*Rhinoderma darwinii*) that nurture their young for extended periods (AmphibiaWeb 2014).

6.8 Concluding Remarks

The assessment of the impact of future climate change on biodiversity has often concentrated on describing the impact of exposure on species future distributions. It has not addressed the influence of species' individual sensitivities in moderating these predicted impacts. This thesis provides robust evidence for what has been theorised in the literature with regards to assessing species' future vulnerability under climate change. This investigation has indicated the factors which confer species sensitivity or resilience to future climate change. The creation of a Sensitivity score has demonstrated that including these factors in the assessment of species' risk to climate change is highly useful. The analysis of the effect of different scenarios of mitigation on avoiding the full impacts of future climate change predicted under a business-as-usual path has provided evidence on the benefit of mitigation on reducing species' vulnerability.

The evidence presented in this thesis demonstrates that species' sensitivity will shape species' vulnerability to future climate change. Further, it has identified the factors which best characterise mammal sensitivity using a statistical method which can be easily replicated for other taxa. It has also identified the regions in which species are predicted to be most vulnerable to future climate change.

Appendix 1: A Review of Species Distribution Modelling

Species Modelling

Ecologists and biologists have strived to understand the distribution of species and the underlying features which determine them for many decades. The field of theoretical ecology to which species distribution modelling belongs has its roots in theories such as the Niche Concept (Hutchinson 1957) and the Theory of Island Biogeography (MacArthur and Wilson 1967).

Species distributional limits are determined by physiological and environmental constraints, i.e. too or not too cold (Guisan and Zimmermann 2000). Thus, climate plays a considerable role in defining species distributions and in controlling ecosystem processes (Pearson and Dawson 2003; Root *et al.* 2003). Observations that changing climates have influenced species distributions are apparent in the fossil record, and in current trends of range expansion and contraction (Pearson and Dawson 2003). This hypothesised relationship between species distributions and the environment forms the basis for predictive ecological models seeking to explore climates effect on species and communities (Guisan and Zimmermann 2000). Patterns of past climate-induced changes in species distributions can aid our understanding of current distributions of species and the genetic variation therein (Hijmans and Graham 2006). As reflected in the past, there are some species which appear particularly vulnerable to losing parts of their range in response to climate change such as mountain-top endemics (Hijmans and Graham 2006). Species distribution models capitalise on scientific knowledge of biophysical and ecophysiological processes and their regulation of species relationships with their environment (Guisan and Zimmermann 2000; Austin 2007). Modelling species, as opposed to communities, is believed to be more realistic because of the short history of modern species communities and the likelihood that communities will not shift as an entire entity (Guisan and Zimmermann 2000). This appendix reviews species distribution modelling techniques and their associated uncertainty

Species distribution models take two main forms, that of correlative or statistical modelling, and that of mechanistic modelling, each form seeks to describe how species distributions are realised. Their power lies in their ability to provide testable hypotheses of species distributions (Guisan and Zimmermann 2000), particularly relevant in the face of global change, climate change (Thomas *et al.* 2004) or otherwise (i.e. land-use change (Sala *et al.* 2000), invasion biology (Vaclavik and Meentemeyer 2009)), and also the accurate prediction of biological patterns (Guisan and Zimmermann 2000).

Ecological knowledge forms the basis of correlative and mechanistic models; it guides the selection of appropriate indicators, whether related to environmental variables or fitness measures (Austin 2002; Guisan and Thuiller 2005). Each of the model types, thus, assumes that it captures the appropriate mechanisms driving a species distribution (Dormann *et al.* 2012). How these indicators are incorporated is what defines both. Correlative models derive functional relationships by fitting species occurrences to environmental data, whereas mechanistic models use knowledge on processes such as reproduction or growth (Dormann *et al.* 2012)

Correlative models use statistics to infer a species' environmental niche requirement from information on their current distribution, and then look for environments analogous to these pre-determined requirements (Pearson and Dawson 2003). They use suites of environmental variables to describe the sites in which the species occur (Wiens *et al.* 2009). As such they are often used to project future occurrences of species based on the presence of the correlated environmental features under future landscape scenarios (Wiens *et al.* 2009).

Process-based mechanistic models build a prediction of a species distribution based on functional traits and physiological traits (Kearney and Porter 2009), such as their life history, physiology, behavioural and genetic plasticity (Wiens *et al.* 2009). These properties govern the species' sensitivity to physical characteristics in their environment (Wiens *et al.* 2009). As such, these models map the species distribution based on locations which are within the species natural tolerance limits (Wiens *et al.* 2009). These models are often used to simulate dynamic features of species distributions, such as the influences of disturbance, land-use change and management on species occurrences (Dormann *et al.* 2012)

Niche Theory

Niche theory forms the conceptual basis in which species distributions models are rooted. Hutchinson described a species ecological niche as a multidimensional space (for which he coined the term ‘n-dimensional hyper-volume’, (Hutchinson 1957)) in which the axes describe the species environmental and resource requirements needed to survive and reproduce (Colwell and Rangel 2009). Within niche theory, Hutchinson defined two niche forms, the *fundamental niche* and the *realized niche* (Hutchinson 1957; Wiens *et al.* 2009). The *fundamental niche* describes the full range of conditions and resources in which a species could survive and reproduce without interference from other species (Hutchinson 1957). The *realized niche* represents a subset of the fundamental niche to which the species is constrained by inter-specific competition and abiotic barriers (Wiens *et al.* 2009). Mechanistic and correlative modelled predictions correspond to different parts of the species niche, where mechanistic models take the fundamental niche as their frame of reference, and correlative models, the realized niche (Wiens *et al.* 2009).

It is widely acknowledged, that although models can never be tested as true or false (Guisan and Zimmermann 2000), because the complexity of the natural world is impossible to capture entirely, they provide a powerful tool for the indication of how species may cope and adapt to future climate change (Pearson and Dawson 2003).

Correlative Models

Ecological niche models, also known bioclimatic or niche envelope models are correlative models which simulate species’ spatial distributions using environmental predictors (Sillero 2011) . Their primary purpose is to describe a species ecological niche rather than to realistically describe ‘cause and effect’ of individual variables (Guisan and Zimmermann 2000), although it is possible to explore general trends in driving factors. These models adopt the general thesis that a species’ current distribution is the best indicator of its climatic requirements and so combine climatic variables with observed distributions in making predictions (Pearson and Dawson 2003; Austin 2007). As such they provide a powerful tool for approximating the impacts of processes such as climate change, as well as evolutionary processes and the impact of alternating conservation strategies (Zimmermann *et al.* 2010).

The theory that climate dictates species distributions at broad geographical scales is widely supported (Pearson and Dawson 2003; Heikkinen *et al.* 2006). This idea stems from that presented by Whittaker (1975), who showed that the distribution of the main biomes of the world can be predicted by the distribution of mean temperature and mean precipitation values. More recent support for the separation out of climate variables for sole use in regional scale distribution models is provided by Thuiller *et al* (2004) who found that models including climate variables held greater explanatory and predictive power than land-cover variables at continental and regional scales.

Although a species' niche space is defined by both scenopoetic and binomic factors, climate processes are recognised as largely controlling a species distribution, shape and its biological properties (Pearson and Dawson 2003). The components that comprise a species' climatic requirements are described as a 'climate envelope', which scientists determine by a species current distribution correlated with its climate variables and the species known physiological responses to climatic changes (Pearson and Dawson 2003). Dormann et al. (2010) found that climatic variables explained 56% of the variation in species occurrences. Climate zones are characterized by their typical ecosystems (Leemans and Eickhout 2004) which in turn are characterized by the species which reside within them.

Ecological niche models thus require information on the species' current distribution and environmental spatial data layers (Elith *et al.* 2006; Graham *et al.* 2008). The known distribution of the species may be inferred from species surveys and museum records (Elith *et al.* 2006). The selection of the predictor variables is based on experience that they show correlations with species distributions, as well as their availability. Predictor variables may not directly influence a species distribution but may act as a surrogate for more nuanced proximal variables (Austin 2007). By combining these data we create a predictive model which statistically associates the distribution data with the spatial habitat data to assess the suitability of any site, globally, by region, or locally, for the species (Graham *et al.* 2008). The resultant climate suitability map represents the probability of occurrence of, or, suitability for occupation for, a species across a pre-determined landscape (Sillero 2011). The species' environmental niche determined by the model can be extrapolated to future climatescapes to determine locations where the species niche requirements are satisfied into the future (Wiens *et al.* 2009). These future climatescapes are derived from climate-change models.

It has been forwarded that correlative models best represent the *realized niche* because they use the species current distribution locations as a representative proxy of the species niche, and this distribution has already been subjected to historical biotic and abiotic interactions (Kearney and Porter 2004; Kearney 2006; Lobo *et al.* 2010). However, it has also been argued that the inclusion of solely environmental variables prevents species distribution models from accurately predicting a species realized niche (Fielding and Bell 1997), as such the output distribution is more akin to the species fundamental niche. This is because additional factors such as, biotic interactions, geographic barriers and geographic and biotic history, are often not accounted for in species distribution models and because species do not necessarily occupy all environmentally-suitable areas (Phillips *et al.* 2006; Pearson 2007a). As a result these predictions are typically larger than the observed realized distribution (Phillips *et al.* 2006). In addition distributions are assumed to represent the species in equilibrium, (i.e. that they occur in all parts of their suitable environmental space) (Dormann *et al.* 2012), when species are rarely in equilibrium with their environment due to dispersal limitations or historical occurrences, is thought to be further evidence that correlative models describe the realized rather than fundamental niche (Lobo *et al.* 2010). As such these models are better thought of as sitting along a gradient between the realized and fundamental niches (Jimenez-Valverde *et al.* 2008), however pinpointing the departure between both the theoretical fundamental niche and realized niche remains impossible and a largely conceptual exercise (Phillips *et al.* 2006).

Correlative models have been used in a variety of applications, such a modelling past, current and future distributions based on the species environmental characterisation gleaned from their current localities (Hijmans and Graham 2006) and representations of past, current and future climates (Pearson and Dawson 2003). Thus, we can estimate changes in the species distributions spatially over time, giving insight into past and future changes under climate change (Pearson and Dawson 2003) . They have been employed to simulate distributions of terrestrial and aquatic plants and animals, vegetation types, biomes and plant or animal biodiversity (Guisan and Zimmermann 2000)

There is a wide variety of correlative model techniques currently in use which vary in statistical mechanism and their potential uses (Guisan and Zimmermann 2000). For instance the model Maxent (Phillips *et al.* 2006), which uses maximum entropy theory, BIOCLIM an envelope model which only uses presence data, LIVES which calculates the species distribution based on distance analysis and the regression-based models GAM (Generalised additive model), MARS-COMM, a regression model based on community data and BRT (boosted-regression tree).

Elith *et al* (2006) conducted a detailed comparison between each of the model algorithms listed on the basis of their ability to predict a range of different individual species distributions. Each model was ranked with regards to its individual performance. The model algorithms performing best across all species were BRT, MARS-COMM and Maxent those with the lowest predictive capacity were BIOCLIM, and LIVES. The worst performing models BIOCLIM and LIVES are both presence only models which do not account for the environmental conditions in which the species occur meaning they are unable to project species occurrences outside the range of the data points. The top performing models are more capable of fitting complex data on the basis of occurrences and environmental data because they employ more advanced algorithm sets to derive the species climatic requirements (Elith *et al* 2006).

Mechanistic

Physiologically-determined mechanistic models present a conceptually alternative way of describing species distributions to ecological niche models (Pearson and Dawson 2003). Mechanistic models find their basis in the processes by which species survive and reproduce; they seek to describe a species distribution on the basis of mechanistic links between the organism's fitness and its environment (Kearney 2006). Ecological knowledge of processes and experimental or observations of processes are used to inform the creation and calibration of processes within the model (Dormann *et al.* 2012). Thus, one begins with the organism in opposition to its distribution and consequently the distribution is mapped based on the fitness consequences of these processes, and their tolerance limits (Kearney 2006). Mechanistic models are thought to model the fundamental niche, by definition this fundamental niche is not an accurate description of the species current distribution, also by describing all individuals as the same they fail to account for individualistic species tolerances and adaptations (Pearson and Dawson 2003). There are two types of mechanistic model- i) 'forward' process-based models, where no parameters are fitted to the object data and ii) fitted process-based models, which involve the calibration of a parameters to a subset of the data (Dormann *et al.* 2012). Mechanistic models are implicitly data hungry incorporating a large number of adjustable parameters, some derived from laboratory experiments, which require validation and calibration against observations (Dormann *et al.* 2012).

Model Comparison

There are positive and negative aspects to both correlative and mechanistic models. One thing which is clear, is that when using either scientists need to consider the resultant model as providing a hypothesis, however informed (Dormann *et al.* 2012). This is because both assume that they correctly capture the significant mechanisms which influence species distributions, but testing these assumptions is beyond the scope of most (Dormann *et al.* 2012).

Each model type can be adjusted to express a greater or lesser degree of generality depending on their ultimate purpose (Guisan and Zimmermann 2000). Guisan and Zimmermann (2000) observe that generality need not be at the expense of reality or precision. When modelling distributions under future climate scenarios a degree of generality is required to allow the model space to extrapolate (Hijmans and Graham 2006). As such, Dormann *et al* (2012) have speculated that correlative models have a greater capacity, in an explorative sense, than mechanistic models, to discover new processes and process interactions, because these are not defined *a priori*.

Data availability often limits the applicability of mechanistic models because they require detailed physiological data and for very few species' dynamic responses to environmental change have been studied, thus, making correlative models the preferred choice where data is scarce (Guisan and Zimmermann 2000). The processing time taken to run each of the model needs also to be considered, mechanistic models commonly take much longer to develop, they also have many more parameters requiring calibration than correlative models which can be quickly employed once environmental and occurrence data is available (Dormann *et al.* 2012). Thus, correlative models can be easily applied to a large number of species quickly, and enable us to draw conclusions about the impacts of environmental change on a suite of species, rather than on an individual species basis (Pearson and Dawson 2003).

Mechanistic and correlative models capture large scale processes to different degrees of precision, depending on focus, however, they both lack the ability to represent subscale heterogeneity accurately (Dormann *et al.* 2012). Thus, they can identify the broad distributional trends, but lack detail, particularly for species whose distributions are fragmented in the landscape (Pearson and Dawson 2003).

Both modelling approaches assume that species are in equilibrium with their environment and as such lack the capability to infer individualistic behaviours such as dispersal ability and adaptive capacity (Guisan and Zimmermann 2000). At the macro-scale, however, evidence for correctly simulated distributions at the continent scale suggests that species are equilibrium with the current climate at this scale (Pearson and Dawson 2003).

Model Selection

Correlative and mechanistic models are thought to sit along a continuum delineated by the degree to which processes are represented in the model (Dormann *et al.* 2012) . Pearson and Dawson (2003) suggested a hierarchical framework describing the environmental-biota relationship based on the variable of interest and geographic scale. Thus, theoretically the analyses should be focused at the scale at which the particular phenomena is dominant (Pearson and Dawson 2003). For example, at the global scale we can consider *Climate* as the dominant factor in defining a species distribution, as such correlative models are the appropriate choice, having the statistical power to produce predictive precision at this scale (Guisan and Zimmermann 2000). Using the hierarchy we can infer the relevant application of the two model types under different scenarios (Table S 1). Selecting the correct model type for the scale of analysis is thus fundamentally important to the success of the model in capturing aspects of the species distribution (Pearson and Dawson 2003). The selection of appropriate subscale processes in large scale analysis, and their subsequent inclusion represents a future challenge for both model types (Dormann *et al.* 2012).

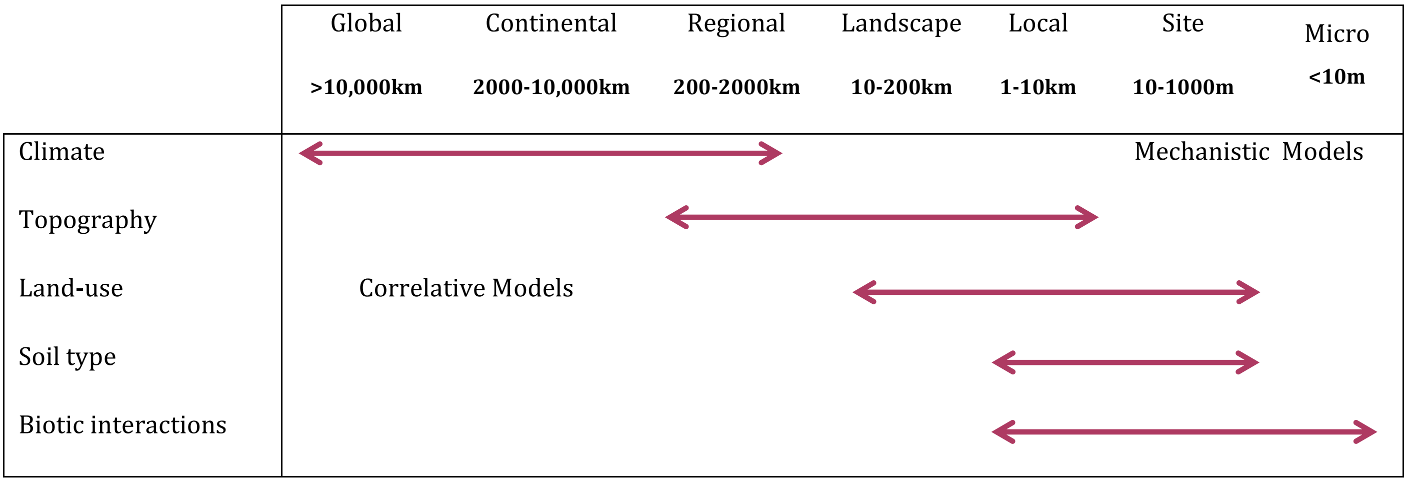


Table S 1 Modelling Hierarchy after Pearson & Dawson, 2003 (Arrows indicate scale of relevance)

Model Selection and Evaluation

Selecting a Correlative Model

The Wallace Initiative in seeking to project a large number of species distributions globally for extrapolation under future scenarios of climate change opted to use a correlative niche modelling approach. Correlative models can be divided into a further three types determined by the type of occurrence data available and ultimate use, these are i) presence- absence, ii) presence-only and iii) presence-'pseudo-absence' (Hirzel *et al.* 2006). In this section each is discussed in relation to their applicability.

Presence-absence data models require occurrence data, where the species has been observed, and absence data which describe locations where the species was observed not to occur (Gormley *et al.* 2011). The preparation of this data requires systematic monitoring of the species to accurately ascertain the species presence or absence within the region of interest (Hirzel *et al.* 2006; Gormley *et al.* 2011). The inclusion of absence data in the model process was observed to add predictive power to the model, because knowing the conditions in which a species is not present is equally relevant to defining the species niche (Wiens *et al.* 2009). However, the observation of 'true' absences is complicated, and a species may be recorded absent where it is actually present, known as a 'false' absence (Wiens *et al.* 2009). Absence data is not commonly available, particularly where species are isolated or have small populations (Graham *et al.* 2008).

Presence-only data models are based solely on occurrence data, as such biotic and historical processes are intrinsic within it, leading to the conclusion that presence-only data predictions most accurately describe the realised niche (Sillero 2011). The ability to discriminate between occupied and unoccupied habitats is unavailable to these models due to the lack of absence data (Sillero 2011). Thus, these models cannot contrast their habitat suitability predictions against patterns of known absences (Hirzel *et al.* 2006). Dependent on the size of the study area and quality and scale of the environmental data presence-only models can predict distributions more or less analogous to the fundamental niche (Sillero 2011). Model accuracy is strongly linked to the number of occurrences and the degree of spatial bias within the data (Elith *et al.* 2006; Graham *et al.* 2008). To circumvent the problem of a lack of absence data, two methods have been suggested, i) the inclusion of generated pseudo-absence data for evaluation, and ii) assessing the models ability to discriminate species suitable climate space (Hirzel *et al.* 2006).

The third type of model uses occurrences and pseudo-absences. Pseudo-absence data is generated to represent absences across the modelled extent of the species distribution model where presence data only is available (Chefaoui and Lobo 2008; VanDerWal, Shoo, Graham, *et al.* 2009). The selection of pseudo-absence data has the power to highly influence the modelled prediction, impacting where the model sits between the realized and potential niche (Chefaoui and Lobo 2008). The technique in which pseudo –absences are selected from the background may affect the model parameterization subsequently impacting the prediction accuracy of the model particularly when projecting in time and space (VanDerWal, Shoo, Graham, *et al.* 2009). Their selection can affect the degree of variability explained, constrain the modelled distribution and inflate the model accuracy (Chefaoui and Lobo 2008). The extent from which pseudo-absences are selected strongly manipulates the model predictions, for instance selecting absences from environmental regions distant from those of the species optimum inflates the model accuracy score and discrimination ability and increases over-prediction (Chefaoui and Lobo 2008). Where absences are selected from an overly broad or restricted region model performance is lower than those selected from an intermediate area around the species presences (VanDerWal, Shoo, Graham, *et al.* 2009). Thus, there is an optimal distance from the species environmental niche requirements which one should stray in the selection of pseudo-absences (VanDerWal, Shoo, Graham, *et al.* 2009).

Presence-absence model techniques were observed to be better able to discriminate species distributions than those which use presence-only data (Chefaoui and Lobo 2008). Where prevalence is low (<50 presences), presence-absence models perform better than presence-only models due to the additional niche information provided by the observed absence data (Hirzel *et al.* 2006). However, absence data should only be employed when the user is certain that absence data has been collected systematically for the area of interest and so is an accurate indication of the unsuitable habitat areas (Chefaoui and Lobo 2008).

Understanding Model Uncertainty

It is important to acknowledge the limitations and uncertainties of species distribution models from the outset if we are to divine meaningful information by their use (Pearson and Dawson 2003; Thuiller *et al.* 2004). There are two broad forms of prediction error, 'algorithmic' error, due to limitations in data-collection and the classification algorithm (i.e. the model equation), and 'biotic' error, which arises from incomplete knowledge and representation of ecologically-relevant processes(Fielding and Bell 1997; Austin 2007). In recognition of such limitations, output of models must be interpreted with care (Pearson 2007a). It is, therefore, important when choosing and developing a model to understand these uncertainties and the various methodologies employed in understanding and reducing uncertainty. Such methodologies include, model validation, analyses of collinearity, autocorrelation, the biased sampling of explanatory variables, scaling and the impacts of non-climatic factors (Heikkinen *et al.* 2006). Since their introduction the focus in correlative modelling has been on the incorporation of alternative drivers of environmental change and biotic processes which interact with climate change, and their effect on species future range shifts (Pearson and Dawson

2003). These alternative drivers and processes involve the inclusion of land cover data, demography, dispersal capacity, and biotic interactions (Heikkinen *et al.* 2006; Wiens *et al.* 2009). Up until recently the incorporation of such drivers was theoretical now models have been adapted to include information on dispersal and demography (Anderson 2013) and how these are shaped by biotic interactions (Araujo and Peterson 2012). These hybrid-models try to incorporate mechanistic properties into normally static correlative models to add further realism to these predictions, and to reduce uncertainty (Heikkinen *et al.* 2006). One example of this is the Dynamic Bioclimate Envelope Model (DBEM) developed by Cheung *et al* (2008) which combines an ecophysiology model, predicting changes in fish growth, with a species distribution model, predicting the future distribution of the fish. Models provide relevant hypotheses when examining the complexities of biological patterns (Guisan and Zimmermann 2000), conferring valuable insight into how to approach future conservation challenges under climate change (Wiens *et al.* 2009).

Biotic Uncertainties

Model performance is heavily influenced by the quality of the model inputs. The primary purpose of species distribution models is to define a species' distribution by defining its niche. Understanding the complexity of species' distributions is notoriously difficult, and the causal drivers which underpin a species distribution are rarely easily quantifiable (Fielding and Bell 1997; Dormann 2007). Thus, models are sensitive to the representation of species' ecological characteristics (i.e. ecological specialisation and range size), within the model process (Brotons *et al.* 2004; McPherson *et al.* 2004; Segurado and Araújo 2004; Elith *et al.* 2006; Hernandez *et al.* 2006). There are several biotic errors common to all species distribution models. Here they are split into those general issues affecting the model process, and, issues which arise due to temporal and spatial extrapolation.

Commonly, environmental variables alone are used to describe a species niche. These variables can include, climatic variables such as annual precipitation and seasonal temperature change, and, categorical variables, for example describing vegetation cover (Hijmans and Graham 2006). Environmental variables, particularly climatic variables, are favoured because they are available at a global resolution and species-specifics are readily defined using species point location data (Hijmans and Graham 2006).

When exclusively using environmental variables to represent climate it is important that they are appropriately scaled because environmental drivers 'differ with their variability and relevance with scale,'(Dormann 2007). It is known that distribution patterns are governed by many factors, not solely climate, and that these influence patterns of distribution but also the rate at which distribution shifts occur (Heikkinen *et al.* 2006). These factors include, but are not limited to, soil type, habitat fragmentation, fire frequency, genetic variation among populations, species dispersal limitations and the impact of climate change (Brotons *et al.* 2004; Heikkinen *et al.* 2006). It is thought that these biotic interactions play only a minor role in governing species distributions at the continental and global scale i.e. >200km but that they are likely to play a more dominant role in defining a species distribution at the local scale, <1km (Pearson and Dawson 2003; Araújo and Luoto 2007).

Species and Non-equilibrium Distributions

A central assumption of correlative distribution modelling is that specie's distributions are in equilibrium with their current climate (Heikkinen *et al.* 2006), i.e. that where suitable climatic conditions exist for the species they will be present (Guisan and Zimmermann 2000). This assumption has brought a large degree of criticism, because in reality species distributions are unlikely to possess this characteristic (Pearson and Dawson 2003). For instance, a species may not be in equilibrium with its environment due to past events from which the population has not recovered for example periodic destruction of habitat by fire or a parasite outbreak, because of its limited dispersal ability (Dormann 2007), biotic interactions and human management (Pearson and Dawson 2003). Conversely, some species' current distributions may represent regions for which the current environmental conditions are no longer viable, a phenomenon termed the "legacy effect" this is commonly associated with species longevity, philopatric behaviours or a species inability to disperse (Wiens *et al.* 2009). This may manifest itself in the absence of individuals in optimal habitats or the species presence in low quality areas (Fielding and Bell 1997; Brotons *et al.* 2004).

As such species' geographic records, and subsequently the associated climate data used for modelling, are unlikely to represent the true extent of a species' niche as a consequence species' future distributions may represent very different realised niches (Pearson and Dawson 2003). Thus, this assumption leaves species-climate model projections vulnerable to bias because the model fails to capture the species' distribution appropriately (Heikkinen *et al.* 2006; Dormann 2007). As such caution should be applied when modelling species where non-equilibrium habitat association is suspected(Brotons *et al.* 2004), because it leaves predictions open to omission and commission errors (Wiens *et al.* 2009). A commission error is where a species is predicted as present where it is absent and an omission error is where a species is present but predicted as absent (Guisan and Zimmermann 2000).

However, to create models which take non-equilibrium situations into account would require dynamic and stochastic functions to be implemented, thus assuming species are in equilibrium is a necessary supposition in the creation of static correlative models (Guisan and Zimmermann 2000). There is evidence that in the creation of large-scale distribution models most species, particularly those from vagile groups, such as birds, are likely to be close to equilibrium as a consequence of their individual habitat selection processes and population dynamics (Brotons *et al.* 2004). Thus, it is suggested that assumption that species distributions are in equilibrium with the current climate at the macro-scale is appropriate (Pearson and Dawson 2003).

Inclusion of Biotic interactions

Most correlative models are calibrated under the assumption that biotic interaction, such as interspecific competition or predation, do not influence species range patterns; or that biotic interactions are only relevant at small scales (Zimmermann *et al.* 2010). There is , however, some evidence that interactions within and between species can impact global model accuracy, for example competition from intraspecifics has been shown to result in species absences from seemingly suitable habitat (Fielding and Bell 1997). The inherent stochasticity of spatial and temporal dynamic processes and on individual's habitat-scale interactions, however, make them exceedingly difficult to quantify for inclusion in species distribution models (Dormann 2007). Although. Araújo and Luoto (2007) found that for their example biotic interactions did influence macro-ecological scale distributions they readily acknowledged that attempting to parameterize and incorporate biotic interactions into macro-scale species distribution models would be an enormous task. Thus, biotic interactions are largely left out of these models because such highly detailed information is rarely available for species (Guisan *et al.* 2006).

Local Adaptations

Species which are widespread are likely to exhibit local or regional specialisation in ecological characteristics as adaptations to subtle differences in their occupied habitat(Brotons *et al.* 2004; Dormann 2007). The modelling of these sub-population nuances in environmental space is likely to result in an inflated projected distribution as a wider range of environmental features and limits are inherited by the model increasing uncertainty (Brotons *et al.* 2004). Hernandez *et al* (2006)found that as tolerance (breadth of environmental space used) broadened, so model predictive accuracy decreased. Conversely, the issue of introducing climatic bias in the prediction created by incomplete sampling of the species environmental space must also be considered (Kadmon *et al.* 2003; Heikkinen *et al.* 2006). Thuiller (2004), showed that the incomplete sampling of the climatic range can strongly influence the estimation of response curves, especially towards upper and lower ends of environmental ranges. To avoid incomplete representation of a species-environmental relationship requires the conscious sampling of the entire gradient of environmental space the species occupies, with particular attention paid to the inclusion of sites at the edge of the species distribution (Heikkinen *et al.* 2006). Accounting accurately for both issues may be overly complex.

Species Dispersal

Understanding and incorporating dispersal into projections of future range shifts will give insight into the ability of individual species to track climate change (Pearson and Dawson 2003). Species which have a large capacity to disperse may be expected to track changing climates and disperse to new areas of suitable habitat within their domain, whereas sedentary species and poor dispersers are likely to be restricted to areas of their current range which remain stable (Pearson and Dawson 2003). However, the ability of species to disperse to their full capacity is dependent on the landscape structure through which they must disperse; habitat fragmentation and natural barriers may thus restrict species dispersal (Wiens *et al.* 2009).

Correlative models inherently suppose that dispersal is not a limiting factor in assuming that the modelled species is in equilibrium within the environment (Vaclavik and Meentemeyer 2009). However, dispersal limitations are known to play a major role in the capacity of species to shift within the environment (Vaclavik and Meentemeyer 2009). Where dispersal mechanisms are represented in model predictions, no dispersal or unrestricted dispersal are the commonly adopted forms, thus they ignore species-specific dispersal abilities (Jaeschke *et al.* 2012). Models incorporating these simplified modes of dispersal have the power to identify future suitable habitats. The assumption of 'full dispersal' or 'no dispersal' in predictions of future ranges provides upper and lower bounds on their potential size, however, both tend to over or under predict species abilities to disperse within the landscape (Jaeschke *et al.* 2012). The inclusion of realistic dispersal could further our understanding of expected future shifts (Jaeschke *et al.* 2012). However, for many species this data is unknown, as such measures of average observed dispersal rates are suggested as a proxy measure of dispersal ability (Lester *et al.* 2007).

Phenotypic and Genetic Adaptation

Correlative models fail to account for the potential for phenotypic and genetic adaptation by species within zone in response to climate change. Correlative models make the assumption that species niches exhibit conservation, i.e. that the species niche is unchanging over time and space (Wiens *et al.* 2009). There is evidence that populations are undergoing phenotypic shifts, where individuals with low dispersal capacity or which are poorly adapted to local climatic conditions are selected against (Pearson and Dawson 2003). Also, although long-lived species with low dispersal capacity are unlikely to display genetic adaptations rapid evolution change in response to environmental change has been observed in species with short-generation times (Wiens *et al.* 2009). Under past climatic change species have been observed to adapt, albeit that adaptation did not occur for all species (Pearson and Dawson 2003). The use of correlative modelling techniques therefore is more appropriate for species with long generation times or poor dispersers which are not expected to undergo rapid adaptive changes (Pearson and Dawson 2003). This is because the mechanism of selection, either between generations or at the expanding range margins, needs to occur for evolutionary processes to happen (Pearson and Dawson 2003).

Recent attempts have been made to represent these ecological interactions in the model process to better represent the mechanisms which serve to underpin species responses to environmental change, and to thus to enhance these models biological authenticity (Wiens *et al.* 2009). The inclusion of biotic variables, their measurement and whether they should be included as predictors in models are challenging topics (Austin 2007).

Model Process Uncertainties

Model predictions are wholly reliant on the conditions under which they are run, the extent of the resolution, the number and scope of the predictors used, and the number and quality of the points making up the dependent variable i.e. the species presences data (Hernandez *et al.* 2006). As such they are inherently uncertain, in part due to the uncertainties associated with the approaches and tools employed (Wiens *et al.* 2009). There has been much research into improving the statistical basis of correlative models to minimise reducible uncertainty, including that inherent in 1) input data, 2) parameter inputs, and 3) model misspecification (Dormann *et al.* 2012). It is, therefore, important when choosing and developing such a model to understand the methodologies employed in assessing model saliency. These include, model validation, collinearity, autocorrelation, the biased sampling of explanatory variables, scaling and the impacts of non-climatic factors (Heikkinen *et al.* 2006). Statistical uncertainty involving, spatial autocorrelation, sampling design, and sampling size and prevalence, have been widely explored (Zimmermann *et al.* 2010).

Environmental Variable creation, selection and collinearity

In selecting variables to represent a species habitat requirements one can draw on the extensive knowledge of ecophysiological and biophysical processes which control species-environment relationships, and which define their distribution (Guisan and Zimmermann 2000; Austin 2007). The effect of variables in influencing a species distribution is dependent on their type, whether direct or indirect, abiotic or biotic, and proximal or distal (Austin 2007). Direct variables include temperature, rainfall and pH, indirect variables for instance altitude and latitude are intrinsically linked with the direct variables, and as such only have an effect in relation to the conditions described by the direct variables (Austin 2007). As such indirect variables are normally used as a simplified proxy of different resource and direct variables (Guisan and Zimmermann 2000). Direct variables and resource gradients are the best choice for modelling at a large scale (Guisan and Zimmermann 2000). Indirect variables cease to have predictive power at these scales because combinations of direct and resource variables will differ at the same topographic position across different regions (Guisan and Zimmermann 2000).

Climate variables for current conditions are constructed using data from weather-stations positioned across the Earth's surface, which are then interpolated taking into account regional topography and local climate anomalies. The creation of climate layers under future scenarios is intrinsically uncertain because of the inscrutable nature of the future (Wiens *et al.* 2009). General circulation models (GCMs) operate under differing parameters and integrate process dynamics such as atmospheric circulation and feedback mechanisms between the land surface and atmosphere using different functions, resulting in divergent hypotheses of future climates (Wiens *et al.* 2009). In using climate variables produced across a suite of GCMs, in what is termed an ensemble model, and taking the average of the projections we can reduce the associated uncertainty (Wiens *et al.* 2009).

It does not necessarily follow that observed correlations between variables and species distributions are the causal factors of the species occurrence, for instance although a species occurrence appears related to mean annual temperature it may not be the direct limiting factor (Dormann *et al.* 2012). Variables more ecologically salient to the species distribution may be overshadowed where other variables better explain variation in the response variable statistically (Heikkinen *et al.* 2006). Multicollinearity, the term used to describe this form of correlation between variables, is therefore one such obstacle to model accuracy. In the case of species distribution modelling, correlations between environmental variables and may obscure the value of individual drivers within the final prediction (Heikkinen *et al.* 2006). Biological knowledge and statistical analysis of the correlation between variables prior to their use will aid the exclusion of highly-correlated variables from the model may reduce this issue (Heikkinen *et al.* 2006; Dormann 2007).

Environmental drivers are usually represented as linear predictors, although it is expected that species responses to actual changes in climate (in terms of abundance or performance) will be non-linear (Austin 2002; Dormann 2007). As such these models fail to account for the complexity of the system and the range of alternatives which small changes in the environmental variables might affect (Austin 2002).

Further selecting the appropriate number of variables is essential to best enhance the predictive power of the model whilst maintaining accuracy (Guisan and Zimmermann 2000). There is inherent risk of overfitting associated with selection of too many variables (Wiens *et al.* 2009). Thus, the selection of the correct explanatory variables, or combination of variables, is one of the most difficult processes in building correlative models (Guisan and Zimmermann 2000). During model building it important to identify the optimal trade-off between creating an underfitted or an overfitted model and to understand what leads to either occurring (Heikkinen *et al.* 2006). Overfitting occurs when there are too many degrees of freedom leaving the model open to the following risks; fitting to irrelevant or inconsistent noise integral in the records, the obscuring of significant behaviour by the spurious variation created by over-parameterisation, and diminished predictive power (Jakeman *et al.* 2006). In the case of species distribution models it is easy to over-parameterize your model by the inclusion of too many explanatory variables upping the models complexity and making it vulnerable to overfitting (Heikkinen *et al.* 2006). More complex models may be perceived to give a better fit statistically, however the predictions they produce may be inferior (Heikkinen *et al.* 2006). In selecting the model which fits the species current distribution most closely there is a risk that it will lose generality to such a degree that it will be less suitable for predicting future distributions under climate change (Hijmans and Graham 2006). Underfitting is the converse problem, where too few explanatory variables are employed and so the model is unable to accurately distinguish the range of conditions within the species niche resulting in lowered predictive ability (Jakeman *et al.* 2006).

There are species distribution models, such as Maxent (Phillips *et al.* 2006), which employ statistical mechanisms to avoid overfitting.

Occurrence Data

Sample size & the importance of sampling design

The quality of the model inputs, i.e. the species occurrence data is paramount to the predictive accuracy of the model, as they are sensitive to the input data's quality and quantity (Wiens, 2009). There is a wealth of occurrence data available from surveys, museums and herbaria, among others, errors are often implicit within these data (Grahams, 2008). Thus, it must be recognised that as available observation data is likely to be a conglomeration of several datasets; data is likely to have been collected for different purposes, at different resolutions, during different time intervals and perhaps under different taxonomic schemes (Dormann 2007). Such differences introduce errors and will have an impact on the models predictive capacity because they introduce misleading information making it difficult for the model to distinguish the species environmental niche accurately (Phillips *et al.* 2006). In a comparison of model projections created using high- and low-quality data, Graham *et al* (2008), found that models may be robust to minor locational errors within the data. Cleaning of the data of highly uncertain locations is thus advised, unless by its removal the reduced sample size will negatively impact the models predictive capacity (Graham *et al.* 2008).

Sample size can impact a models ability to discriminate accurately suitable environmental space for a species in several ways (Heikkinen *et al.* 2006). It is recognised that as sample size increases the level of uncertainty associated with parameter estimates decreases eventually reaching an asymptote referred to as the models maximum accuracy potential (Hernandez *et al.* 2006; Wisz *et al.* 2008). The sample size at which the asymptote is reached and at which the maximum accuracy potential is achieved will depend on the species, the study area, the spatial resolution of the environmental variables, the quality of the observation data and the model method itself (Hernandez *et al.* 2006). Those species with narrow tolerances niches may be described with few observations, however, for species with broader tolerances few samples are unlikely to describe accurately the range of conditions over which the species might occur accurately (Kadmon *et al.* 2003; Wisz *et al.* 2008). Small sample sizes where the species niche is not fully described can reduce the predictive capacity of the model (Hernandez *et al.* 2006; Phillips *et al.* 2006). This type of data paucity arises not because the species is rare but perhaps because it is difficult to sample (Wisz *et al.* 2008) . It is important to note, however, that not all species with narrow tolerances and few observations will be accurately modelled. Species occupying a micro-habitat or restricted to a geological formation are often inaccurately modelled because their niche requirements are unlikely to be distinguished by climatic information (Hernandez *et al.* 2006). With small sample sizes the influence of outliers also increases because they carry more statistical weight, skewing the statistical analysis, however, where more data is available this effect is buffered (Wisz *et al.* 2008). Paradoxically, large sample sizes can also be a hindrance to model accuracy. Overly large sample sizes, where little is contributed to the definition of the species niche with the additional information also can compromise the models predictive ability (Heikkinen *et al.* 2006). When data consists of thousands of data points it is easy to obtain statistical significance even though the predictors account for only a minor part of the variation in the species distribution data (Heikkinen *et al.* 2006). Thus, when dealing with large data sets caution needs to be applied in order to avoid over-parameterization in including environmental variables which contribute little of ecological relevance (Heikkinen *et al.* 2006).

Contiguity and Marginality

Species tolerance or marginality is known to influence model accuracy (Brotons *et al.* 2004; Elith *et al.* 2006; Heikkinen *et al.* 2006). Studies have shown that species niche breadth is negatively correlated with model accuracy; species with the combined distributional attributes of high prevalence and a limited range of climatic conditions are more precisely modelled than those rare species inhabiting a broad range of environments (Kadmon *et al.* 2003; Brotons *et al.* 2004; Heikkinen *et al.* 2006). Furthermore, species with distributions that are highly spatially contiguous are better modelled than those exhibiting low contiguity (Heikkinen *et al.* 2006). However, when defining the model, the use of an inappropriate spatial extent of analysis can unintentionally inflate model accuracy (Elith *et al.* 2006). Elith *et al* (2006)explained that where the spatial extent is fixed, for example by region, and the species evaluation data is highly contiguous over a subset of space, then the evaluation dataset will have many zero records across the region. Thus, any model able to accurately restrict its non-zero predictions to the zone the species occupies will produce a good AUC score due to the comparison with the numerous absence sites (Elith *et al.* 2006). Broton's et al (2004), established that models for highly tolerant and wide-ranging species were more statistically-sensitive to absence data. As such they suggest that employing presence/absence models to model these species may be more suitable than presence only. Importantly, model accuracy is not only a function of the number of presence records available, but greatly more complex (Elith *et al.* 2006).

Spatial Autocorrelation

Spatial autocorrelation which is the 'tendency of neighbouring sample units to possess similar characteristics' causes the assumption of independence between samples to be violated (Guisan and Zimmermann 2000). Spatial autocorrelation can arise because the variables used by the model do not fully reflect the 'choices' available to the animal, in this case it is the residuals from the fitted model which exhibit spatial autocorrelation (Fielding and Bell 1997). This form is problematic when applying test statistics, and is classified as an algorithmic error because inappropriate variables were selected (Fielding and Bell 1997).

Spatial autocorrelation will also be apparent when species observations are clustered in space (Pearson and Dawson 2003). This clustering is often an artefact of the observers sampling scheme, for instance observations may be clustered around field camps or settlements (Pearson and Dawson 2003; Phillips *et al.* 2006). Clustered data points are usually more similar to one another than those more distant points, biasing the sample (Dormann 2007). Test statistics are thus vulnerable to inflation because species points are not spatially independent (Pearson and Dawson 2003).

Validation

Validation is the process by which we test the accuracy of model prediction using testing data. Testing data is a portion of the original occurrence data which is set aside, and, not used for model building or calibration during the initial training run, for the purpose of validation (Guisan and Zimmermann 2000). This form of validation is often referred to as cross-validation. Further validation methods include assessing the specificity and sensitivity (Dormann *et al.* 2012). Sensitivity is a measure of the proportion of the actual positives, i.e. the presence of the species, which the model correctly identifies. Specificity measures the proportion of actual negatives i.e. the true negative rate, which is the proportion of negatives or species absences which are correctly identified as such by the model. Thus, a model which made a perfect prediction would be 100% specific and 100% sensitive, correctly predicting all actual presences and all actual absences (Dormann *et al.* 2012).

Extrapolation Issues

There are several important caveats to recognise when wishing to extrapolate beyond the species current distribution in space and in time. Specifically of interest is how environmental changes will impact species distributions.

The unavoidable spatial uncertainty of environmental change scenarios naturally complicates the prediction of future species distributions. In projecting species distributions in to the future it is likely that species will be confronted with a set of environmental conditions never before encountered (Thuiller 2004). Where climate surfaces present sets of environmental conditions for which there is no modern analogue then modelling results are incomplete because the model cannot predict how a species will 'cope' under novel climate conditions (Heikkinen *et al.* 2006). Even with the inclusion of environmental and biotic traits trends, data may no longer be valid when applied beyond the range of the data (Dormann 2007). For example biotic interactions recorded at T1 may no longer be valid at T2 under climate change (Araújo and Luoto 2007). Also, a species may be adapted to conditions outside of the range in which it is currently found, but not exist in the region where this combination is found, thus, a correlative model may classify these regions are unsuitable (Hijmans and Graham 2006). These models also assume that variables and processes will interact in the future as they do currently (Dormann *et al.* 2012). Individual species inherent flexibility to adapt to environmental change is as yet unclear, a species intrinsic phenotypic plasticity, or ability to evolve and adapt may mean it is able to maintain a viable population under such change (Dormann 2007). When extrapolating into the future, statistical testing on independent training and testing data can no longer be performed as there is no observed data unlike models for current observations adding to further uncertainty in the projections (Hijmans and Graham 2006).

Verification and Statistical Testing

The procedure of verification is carried out to test that the model has been implemented technically correctly; this term is somewhat erroneous as the nature of models as hypotheses means they cannot be verified as correct (Dormann *et al.* 2012). However, insofar as a model can be verified the verification process seeks to ensure that pre-processing, settings and assumptions have been accurately specified within the model (Dormann *et al.* 2012).

It is difficult to evaluate models based on presence-only data because there is no absence data on which one can evaluate the rate of commission errors (false positive predictions) (Hernandez et al, 2006). However, there are several statistical techniques that have been employed (Fielding and Bell 1997; Heikkinen *et al.* 2006). The inclusion of pseudo-absence or background data, as in Maxent, simplifies statistical model testing to some degree (Phillips *et al.* 2009). Commonly, one of two statistical measures is used, the Kappa statistic, a threshold dependent measure, or the area under the curve (AUC) of a receiver operating statistic (ROC) plot, a threshold independent measure (Heikkinen *et al.* 2006).

Threshold Dependent Measures: Kappa Statistic

Kappa is a threshold-dependent measure determined using a Confusion Matrix (Fielding and Bell 1997). The Kappa coefficient measures the proportion of specific agreement, i.e. the proportion of correctly classified presences and absences once the likelihood of chance agreement has been excluded (Heikkinen *et al.* 2006). The degree of concordance based on Kappa can be measured as, poor K <0.4; good 0.4<K<0.75 and excellent K 0.75> (Fielding and Bell 1997). Kappa is dependent on a single model-generated threshold criterion to distinguish between predicted presence and predicted absence (Heikkinen *et al.* 2006). In the case of presence- only models this continuous variable is the likelihood of a species presence which falls between 0-1, the threshold defines at what value above which the model classifies a presence and vice versa for an absence (Heikkinen *et al.* 2006). The model may automatically generate a threshold at which it classifies a species to be present or absent or one may be set, such a process is felt to be largely subjective (Lobo *et al.* 2010). The availability of the raw scores generated by the model allows closer examination of the data to which the threshold will be applied (Fielding and Bell 1997). Larger thresholds tend to decrease commission errors but increase omission errors (Hernandez *et al.* 2006).

There are several reasons why examination of the threshold value is important, for instance, unequal group sizes (prevalence) could influence the scores generated by some classifiers (Fielding and Bell 1997). The robustness of Kappa has been questioned on the basis that it requires a threshold to be defined in order to be calculated, and the methods under which the threshold is calculated will influence Kappa (Heikkinen *et al.* 2006). Although dichotomous presence- absence classifications are attractive to decision makers they can introduce distortions such as bias (Fielding and Bell 1997). However, there have been advances in the process through which thresholds are selected in converting continuous data into presence-absence scores (Lobo *et al.* 2010). For instance, Lobo *et al* (2010) recommended allowing Kappa to define the threshold, known as the Kappa-maximised threshold, thus, circumventing the question of whether or not the threshold set is appropriate. Liu *et al* (2013) investigated mathematically and empirically the suitability of different threshold selection methods. They found that Max SSS (based on maximising the sum of both sensitivity and specificity) had the best performance scoring higher sensitivity than the other methods in most cases and giving higher kappa than the other methods.

An alternative solution to threshold adjustments is to make use of all the information contained within the original continuous variable and calculated threshold independent measures (Fielding and Bell 1997).

Threshold Independent Measures: AUC

Threshold-independent evaluation statistics do not require a threshold to be set to be calculated. The most commonly used of these is the Area under the Curve (AUC) of the Receiver Operating Curve (ROC) (Lobo *et al.* 2010). The ROC plot is created by plotting all correctly classified cells (the true positive proportion) against the equivalent incorrectly classified cells (false positive proportion) on the y-axis, across a range of threshold levels on the x-axis (Fielding and Bell 1997; Heikkinen *et al.* 2006). As such the ROC takes into account both commission (false positive prediction errors) as well as omission errors (false negative prediction errors) (Hernandez *et al.* 2006). The AUC is an important statistic as it provides a single measure of the overall model accuracy but is not dependent on a single threshold value avoiding the subjectivity of threshold selection (Fielding and Bell 1997; Lobo *et al.* 2010).

AUC values typically fall between 0.5 and 1.0, if the score is 0.5 this indicates that the model tends to predict presences which are in fact absences (Heikkinen *et al.* 2006). Below 0.5 then the models prediction is no better than random. A value of 1.0 indicates that the model is distinguishing perfectly between presences and absences; typically AUC values do not reach this level (Fielding and Bell 1997). By way of an example, an AUC value of 0.8 is interpreted as meaning that 80% of the time ' a random selection from the positive group will have a score greater than a random selection from the negative class' (Fielding and Bell 1997).

Lobo *et al* (2010) questioned the validity of using AUC to measure model accuracy on the basis that; 1) it doesn't account for the predicted probability values or model goodness of fit; 2) omission and commission errors are weighted equally; 3) the test performance is summarized over rarely used regions of the ROC space ; 4) information about the spatial distribution of model errors is obscured; and, most significantly 5) the spatial extent over which models are run impacts the rate of well-predicted absences influencing the AUC score.

The calculation of AUC, because it is a discrimination index, ignores the raw probability scores of the model (Lobo *et al.* 2010). It assumes that presences will have higher predicted values than absences regardless of how well the model has fit the data which can result in poor-fitted models displaying good discrimination power (Lobo *et al.* 2010).

AUC weights omission and commission errors equally, when depending on the model application, they may not be of equal importance (Lobo *et al.* 2010). For instance, when searching for a new species or populations low omission errors are desirable, whereas when designing a reserve misclassification of commission errors are a more serious weakness (Lobo *et al.* 2010). This can be rectified by the implementing of a threshold at the point where the desired balance between commission and omission errors is achieved for the model purpose (Lobo *et al.* 2010).

Thirdly, ROC plots summarize test performance over the whole range of available ROC space because it accounts for all the information within the predictive model (Lobo *et al.* 2010). Researchers typically are interested in one or few points over this space, for instance the extreme left and right sides of the plot- representing high false-negative and high false-positive rates respectively, are generally useless (Lobo *et al.* 2010). Lobo et al (2007) argue that apparent absences may be an artefact due simply to the low detectability of a species or may correspond to non-sampled areas, meaning false-absences are more likely to occur than false-presences as such commission errors should not weigh as much as omission errors.

ROC does not reveal information about the distribution of spatial errors within the model, a common error among all single-number calculations of accuracy (Lobo *et al.* 2010). As such it impossible to know whether errors are spread homogenously across the modelled territory, or if the fall in model accuracy is due to its inability to predict correctly a specific region (Fielding and Bell 1997; Lobo *et al.* 2010).

Finally, and most significant, models that over-predict presences will display a low commission error if the prevalence of absences is much higher than that of presences which is a consequence of the spatial extent selected. This scenario may artificially inflate the AUC score if the spatial extent is inappropriately large for the scale of the distribution (Lobo *et al.* 2006). This is particularly apparent where a constant extent, for instance a region, is used when modelling a specialist species which by its nature only exists in a subset of the region (Elith *et al.* 2006). Hernandez *et al* (2006) found that marginality was indeed positively correlated with AUC scores. Models which can restrict non-zero predictions to the species zone will thus have a good AUC score because of the many absence sites within the evaluation data (Elith *et al.* 2006). Thus, using a constant extent for a variety of species' may not always be appropriate, and consideration must be given to the end use of the model predictions (Elith *et al.* 2006).

Despite these recognised problems AUC remains one of the most prevalent measures used by species distribution modellers, as one of the few model accuracy measures available. Further model evaluation techniques, such as bootstrapping and jackknifing, which are related resampling methods, can complement the use of independent measures such as AUC (Guisan and Zimmermann 2000).

Conclusion

Despite the inherent uncertainty implicit in species distribution models, particularly when extrapolating into the future, their outputs provide us with valuable insights into the future impacts of climate change on species. Thus, these models are extremely useful as long as one is aware of the caveats associated with these models taking steps to minimise their influence. The insight these models provide will assist conservationists and policy-makers in planning future conservation methods which are appropriate.

Appendix 2: The Wallace Initiative and Species Distribution Modelling Techniques

Maxent: Species Distribution Modelling

The species distribution model, Maxent (Phillips *et al.* 2006) was chosen for use in the Wallace Initiative because it has been repeatedly cited as having a strong performance when tested against other presence-only distribution models (Elith *et al.* 2006; Hernandez *et al.* 2006; Pearson 2007a; Wisz *et al.* 2008). Maxent is a presence-only species distribution model which works on the statistical principle of maximum entropy to make predictions from presence-only data (Phillips *et al.* 2006).

The principle of maximum entropy is that it 'agrees with everything that is known [i.e. that inferred from the environmental conditions at the occurrence localities], but carefully avoiding anything that is not known,' (Jaynes 1991; Phillips *et al.* 2006). By way of illustrating the concept of entropy, Professor Brian Cox uses the analogy of a sand pile versus a sandcastle (Cox 2011). The sandcastle exhibits low entropy, because there are few ways of organically re-arranging the sand grains within its structure to recreate the identical sandcastle. The sand pile, however displays high entropy because there are many ways of re-arranging the constituent grains within its structure to recreate it. The model Maxent seeks to maximise its predictive capacity of species distributions by reducing uncertainty associated with the environmental variables. Thus, in Maxent's case, entropy is defined as a measure of the uncertainty connected with a random variable (Phillips *et al.* 2006). The maximum entropy probability distribution describes the modelled species distribution which exhibits the lowest entropy in synchrony with the maximised distribution (Phillips *et al.* 2006). The process by which Maxent creates its predictions is described in more detail below.

Maxent uses the environmental and location information provided to estimate a probability distribution across the study area which satisfies a set of constraints determined by the occurrence data (Phillips *et al.* 2006). These constraints are imposed across the environmental predictor variables and represent the mean value and associated confidence interval as determined by the mean over the presences (Guisan *et al.* 2007). The model by probabilistic reasoning then chooses from the manifold probability distributions satisfying the set of constraints, which maximises entropy (i.e. that which is closest to uniform) (Phillips *et al.* 2006). By choosing the distribution which displays maximum entropy the model avoids placing any unfounded constraints on the final predicted distribution (Pearson 2007a). The complexity of the Maxent model can be modified to suit the species data by the choice of fitted functions, known in Maxent as feature types (Elith *et al.* 2006), these are further discussed below.

Maxent is similar to logistic regression in that it weights each input variable (environmental variable) by a constant (Hernandez *et al.* 2006), creating Features. It then estimates an exponential probability distribution to the sum of the Features, this value is subsequently divided by a scaling constant so values fall in the range 0-1 and sum to 1 (Hernandez *et al.* 2006). These values indicate the likelihood of species occurrence. The model undergoes an iterative process, starting with a uniform probability distribution; it systematically alters the weighted variables until the likelihood of the occurrence in the dataset is maximised (Hernandez *et al.* 2006). That probability distribution(the modelled potential species distribution) which best satisfies the environmental constraints initially imposed by the occurrence data of the species, whilst representing the greatest distribution range (Phillips *et al.* 2006). The output is deterministic because the Maxent algorithm does not use randomness meaning that the resulting output will always be the same given the same starting conditions (Hernandez *et al.* 2006).

Maxent has been shown to combine excellent predictive ability and moderate sample sensitivity (Wisz *et al.* 2008). Elith et al (2006) proposed that the ideal model algorithm would output predictions with high accuracy (i.e. as validated by high AUC values) and demonstrate low variability across species. Maxent was described by (Hernandez *et al.* 2006), as performing well, remaining fairly stable in its predictive accuracy and the total area predicted when tested against a range of sample sizes. Maxent's consistent performance across a range of sample sizes was again highlighted by Wisz et al (2008), who found that it outperformed a number of other models at low sample sizes (10 unique points) and was bested by only one other model at high (100 points) and intermediate (30 points) sample sizes. Maxent has also been assessed as robust to a moderate degree of error implicit in the locational data, able to produce meaningful projections of the species distribution (Graham *et al.* 2008). This ability of

Maxent to perform well at low sample sizes has been put down to its regularization procedure which counteracts the tendency to overfit models at low sample sizes (Hernandez *et al.* 2006). The use of linear regularization in Maxent avoids overfitting but encourages parsimony because it tends to produce models with few non-zero coefficients (Phillips and Dudik 2008). Maxent's good performance may be a function of the generative rather than discriminative approach it uses, modelling the species distributions directly. This generative approach may go some way to explaining its success with small amounts of training data, as generative methods have been found to outperform discriminative (regression) models at small sample sizes (Phillips and Dudik 2008). Phillips and Dudik (2008), state that Maxent may outperform regression methods such as GAMs and GLMs when using presence-only data because regression-based methods use background data taken from across the model space to use as absence data when it may be contaminated with presences, contaminating the control.

This appendix seeks to illustrate the model process by which predicted species distributions were created in the Wallace Initiative. It gives an explanation of the inputs required, the basis for decisions taken and likely outputs created within the modelling exercise.

The Wallace Initiative

The Wallace Initiative's raison d'être is to provide detailed analysis of species distributional changes under climate change. It provides a comprehensive examination of 48786 species of animals and plants globally, and uses a consistent set of global climate scenarios for all the projections (Warren *et al.* 2013). Salient to this investigation are the 5351 animal species projections, representing 1161 mammals, 3042 birds, 487 amphibians and 661 reptiles (Warren *et al.* 2013).

Species distribution models require two inputs to run, the species distribution data and the explanatory environmental variables. In the case of the Wallace initiative primary biodiversity data was sourced from the Global Biodiversity Information Facility GBIF,(GBIF 2013) and environmental variables were projected using a form of probabilistic modelling.

Occurrence Data: The GBIF database

Species observations data are sourced from the Global Biodiversity Information facility GBIF (GBIF 2013) database which holds a huge amount of species occurrence data (c. 417,863,900 occurrence records of 1,426,888 species) from across the globe, from many international collaborators (GBIF 2013). Inaccuracies in such a large database are inevitable, particularly in relation to the location referencing which may be unavailable, wrong, or present inaccurate coordinates (Warren *et al.* 2013). As such before the data's use in the Wallace Initiative model it undergoes a computerised cleaning process consisting of three levels; 1) removal of records with no location data or which did not fall on a land area; 2) removal of occurrences which did not match the reported country of origin ; 3) removal of points considered as outliers based on the species niche requirements (Warren *et al.* 2013) . It is also important to note the lack of species coverage in GBIF, particularly in China and Russia when engaging in a global analysis of species trends (GBIF 2013). Another issue arises in the taxonomic identification of species records, inaccuracies in species identification could introduce a bias into the results, however, it is thought that this is unlikely due to the random spread of such errors (Warren *et al.* 2013) .

The Environmental Variables

In the Wallace Initiative selection of the appropriate variable set is decided based on the number of unique occurrence points; for species with fewer than 40 points 4 variables are used, for those above 40 points 8 variables are used(Warren *et al* 2013). The Wallace Initiative variable sets were selected as they are most likely to impact species distributions across a broad range of taxa; they are also commonly used in publications (van der Wal, pers.comm). The eight environmental variables are created from downscaled climate projections using an ensemble of seven general circulation models representing six alternative greenhouse gas emission scenarios, and at 0.5°x 0.5° scale (Warren *et al.* 2013). These variables are then post-processed to provide the bioclimatic indices required and include: annual mean temperature, temperature seasonality, maximum temperature of warmest month, minimum temperature of coldest month, total annual rainfall, rainfall seasonality, maximum temperature of the hottest month, minimum temperature of the coldest month, rainfall of the wettest quarter and rainfall of the driest quarter.

The Wallace Initiative Modelling Process

The model used to predict current and future species distributions is the presence-only method Maxent (Warren *et al.* 2013). As earlier highlighted, Maxent is considered to be one of the most robust forms of presence-only species distribution models currently available (Elith *et al.* 2011).

The model is used initially to predict the species current distributions using presence data. The first procedure implemented trains the model; this stage estimates a probabilistic distribution of the species' current geographic distribution using observed data points from GBIF. This process derives the relationship between the species presences and the environmental variables. The higher spatial resolution 10 arc-minutes Worldclim environmental indices (Hijmans *et al.* 2005) were employed in this initial stage so as not to lose information about species environmental requirements (Warren *et al.* 2013). This is particularly relevant when modelling species with small distributions, for instance an endemic species occurrence points may be clustered with a 0.5°X0.5° cell, but represent a series of differing environmental conditions (van der Wal, pers. comm.). Only taxa with at least 10 unique geographically unique observation points were modelled, all eight environmental variables were utilised as driving variables for species with over 40 unique points. A subset of four (including Annual mean temperature, Temperature seasonality, Total annual rainfall and rainfall seasonality) were used for species with 10-39 observations (Warren *et al.* 2013). These variable sets were selected because they are thought to best represent the variables which drive species distributions across a broad range of taxa (van der Wal, pers. comm.).

The second procedure calculates the species actual distribution for all global land areas using the derived species-environment relationship. These predicted 'current' distributions are constrained by two factors; a 2000km buffer around the occurrence records including any oceanic islands within it, and the limits of the specie's biogeographic region (as defined by Olson *et al* 2001). The sizeable 2000km buffer was set to avoid omission errors owing to the likely paucity of the GBIF data whilst simultaneously minimizing commission errors by preventing species being predicted as present in widely separated regions with similar climates (Warren *et al.* 2013). Applying such a large 2000km buffer could result in overestimation of species current distributions, especially for more localised species, however, when projecting in to the future its avoids the model predicting dispersal into areas already occupied by the species current distribution (Warren *et al.* 2013). The biogeographic zones are listed as Palearctic, Nearctic, Afrotropic, Neotropic, Australasia, Indo-Malaya, Oceania and Antarctic (Olson *et al.* 2001). Implementation of the zonal buffer, for example, prevented European species being predicted in North America which is likely due to the similarity in climatic conditions (Warren *et al.* 2013). The predicted distribution is thus constrained to climatically suitable habitats within the buffered region.

Ten cross-validated runs were performed for each species as a way of reducing uncertainties and assessing Maxent's prediction accuracy (Warren *et al.* 2013). The Maxent default settings were unaltered because they have already undergone optimization routines for a broad range of species, globally (Phillips *et al.* 2006; Phillips and Dudik 2008). Finally the trained model was re-projected onto the set of 42 climate scenarios at the time points 2020, 2050 and 2080 (Warren *et al.* 2013). This part of the process estimates the species geographical position following a change in climate, by essentially finding the future position of the species climate envelope.

The Wallace Initiative projects the species under three different dispersal scenarios, null dispersal, realistic dispersal and optimistic dispersal (Table S 2). The 'Realistic' and 'Optimistic' dispersal scenarios were determined from the available literature on dispersal for the taxon and represent, for the 'realistic dispersal' the 'average' reported dispersal value and the highest value reported as the 'optimistic' rate (Warren *et al.* 2013). The Wallace Initiative did not create projections using a full dispersal scenario because it is considered to be unrealistic (Warren *et al.* 2013).

	Dispersal Mechanism (km/yr)					
	Null Dispersal		**Realistic Dispersal**		**Optimistic Dispersal**	
Taxa	km/yr	km/100yr	km/yr	km/100yr	km/yr	km/100yr
Amphibians	-	-	0.1	10	0.5	5
Birds	-	-	1.5	150	3	300
Mammals	-	-	1.5	150	3	300
Reptile	-	-	0.1	10	0.5	5
Plants	-	-	0.1	10	0.5	5

Table S 2 Dispersal rates by Dispersal Mechanism (defined in the Wallace Initiative (Warren et al 2013))

The Realistic dispersal rate represents the 'most likely' scenario, and comprises of estimated rates of yearly dispersal for each of the taxon modelled, multiplied by the number of years into the future being projected (Table S 2). Data on individual species' dispersal capacities is sparse therefore averages are taken across the available information on dispersal capacity by taxon to estimate a representative rate (Warren *et al.* 2013). Warren *et al* accept that dispersal rates may vary significantly within taxa. These dispersal scenarios were applied in the form of a buffer around the current distribution with dispersal only able to occur over contiguous land areas within the same biogeographic zone.

Performance Indicators

The Wallace Initiative uses AUC (Fielding and Bell 1997) to test the model performance for each species before projection across the climate scenarios. A cross-validated performance of AUC>0.7 is considered to indicate a good performance, as such species-specific models attaining this level underwent the full projection process as described above (Warren *et al.* 2013).

An Illustrative Case Study in using Maxent

The Maxent Model

As part of this model analysis I have undertaken to create a case study in order that I can draw my own conclusions on the most appropriate method to run Maxent to produce the best estimates of future climate space for a large number of species. I carried out this study to gain further insight into the mechanisms available for use in Maxent in the production of predictions of future suitable climate space for species. As in the Wallace Initiative, this example uses the presence-only species distribution model Maxent. The model runs employ the Maxent default settings, with the exception of the case in which I explore the regularisation setting, a form of statistical relaxation which controls the flexibility inherent in the model prediction (see detail on the Maxent Model above). The Maxent model is run in R using the R package Dismo (Hijmans *et al.* 2013), rather than directly through the Maxent Interface to allow for further processing.

Model Inputs and their Preparation

Occurrence Data

The quality of the model inputs is paramount to the predictive accuracy of the model which is sensitive to the input data's quality and quantity (Wiens, 2009). Occurrence data used in this illustration were sourced from the GBIF, (GBIF 2013) database, and consist of 51080 geographically-referenced occurrence points from the distribution of the European Common Frog (*Rana temporaria* Linnaeus, 1758*)*. The Common Frog's actual distribution and GBIF occurrence points are shown in Figure S 1. The data underwent initial cleaning to remove non-geographically referenced records and to introduce uniformity into the taxonomic information. Further cleaning of the data was undertaken so it consists of geographically-unique occurrence points only; this additional step reduces the number of data points to 24067.

a) Current Distribution of the Common Frog (*Rana temporaria*) (Kuzmin *et al.* 2012)

b) Occurrence data for the Common Frog (GBIF, 2013)

Figure S 1 Common Frog (Rana temporaria) a) Distribution and b) Occurrence records in the GBIF database

Environmental Variables

The selection of an appropriate set of environmental variables which are relevant to the species distribution is critical (Phillips *et al.* 2006). Maxent is able to utilise continuous data, arbitrary real values corresponding to measured values such as maximum temperature and precipitation, and categorical data representing a limited number of discrete values such as vegetation type , for the creation of features (Phillips 2008). Features form the constraints within which the model must perform, and are simple fractions of the environmental variables (Phillips and Dudik 2008). Each of the environmental variables must have the same spatial extent and resolution (Phillips 2008)

The environmental climate grids used in this analysis are the Bioclim grids hosted by WorldClim (Hijmans *et al.* 2005). The grids are created using interpolated data collected from weather stations across the globe, including 47,554 stations recording precipitation data, 24,542 recording mean temperature, and 14,835 recording minimum and maximum temperature (Hijmans *et al.* 2005). Current projections are derived from monthly data over the period 1950 to 2000. Future projections are created using bioclimatic variables created using climate surfaces created by the Wallace Initiative using Met Office HadCM3 (Met Office 2006) climate projections under the SRES A1B scenario.

The three bioclimatic variables sets used in this study Table S 3 reflect the two subsets used in the Wallace Initiative of 4 and 8 variables, with the addition of analysis with the full set of 19 variables to explore how the number of variables impacts the predicted distribution Table S 3. The degree to which the number of variables included will affect the final result is dependent on how correlated the included variables are (Hijmans and Graham 2006). Maxent has the ability to select appropriate variables or weight them meaning that the model is less prone to overfitting the occurrence data (Hijmans and Graham 2006). Although Maxent will identify the most salient variables for use for individual species distributions it is unclear how to automate this for a large number of species as required for the Wallace Initiative calculations (van der Wal, pers. comm.). This case study explores the crossover of ranked variables in the 8 variable set with those Maxent ranks as most influencing the Common Frog's distribution.

Environmental Variables	**Code**	**19 Variables**	**8 Variables**	**4 Variables**
Annual Mean Temperature	BIO1	▨	▨	▨
Mean Diurnal Temperature Range*	BIO2	▨		
Isothermality	BIO3	▨		
Temperature Seasonality	BIO4	▨	▨	▨
Max Temperature of Warmest Month	BIO5	▨	▨	
Min Temperature of Coldest Month	BIO6	▨	▨	
Temperature Annual Range	BIO7	▨		
Mean Temperature of Wettest Quarter	BIO8	▨		
Mean Temperature of Driest Quarter	BIO9	▨		
Mean Temperature of Warmest Quarter	BIO10	▨		
Mean Temperature of Coldest Quarter	BIO11	▨		
Annual Mean Precipitation	BIO12	▨	▨	▨
Precipitation of Wettest Month	BIO13	▨		
Precipitation of Driest Month	BIO14	▨		
Precipitation Seasonality	BIO15	▨	▨	▨
Precipitation of Wettest Quarter	BIO16	▨	▨	
Precipitation of Driest Quarter	BIO17	▨	▨	
Precipitation of Warmest Quarter	BIO18	▨		
Precipitation of Coldest Quarter	BIO19	▨		

Table S 3 Environmental variable sets

* (mean of monthly (max temperature – min temperature)

Model Output

This section describes the Maxent model outputs both in terms of the predictions of current distribution in the form of maps and also the statistical validation process. It also examines the impact of using different combinations of input variables in determining the current distribution and future suitable climate space. It is illustrated using the results created in this study of the Common Frog.

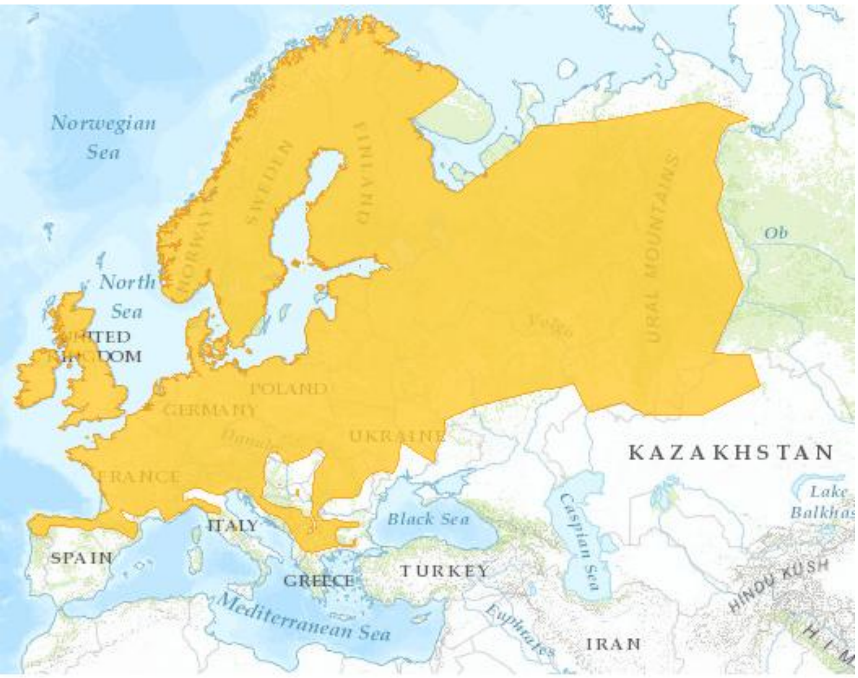
Maxent Log, Cumulative and Raw Outputs and associated maps

Maxent can produce three differing output formats from the model values; these are raw, cumulative and logistic. The three are monotonically related, they thus result in an identical performance when measured with rank-based statistics, such as AUC, because site areas ranked in the same order across the outputs (Phillips and Dudik 2008). The differences lies in the scale applied to the model values; as such each has a different interpretation (Phillips and Dudik 2008). However, this is not true for measures of predictive performance which depend directly on the actual output values, such as Pearson's correlation, will report varying levels of predictive performance (Phillips and Dudik 2008).

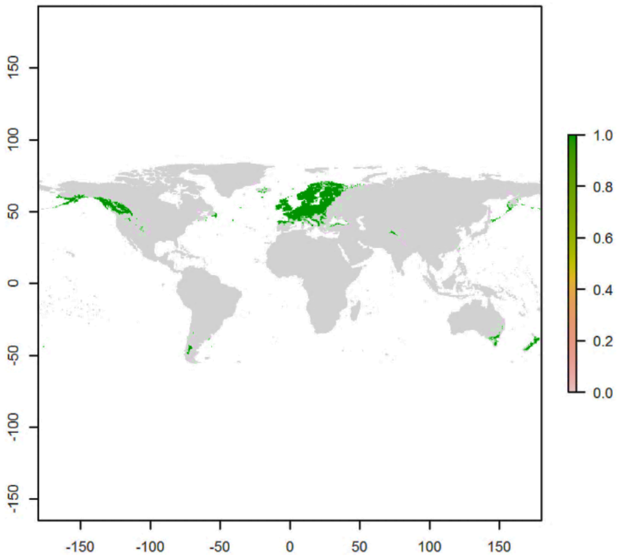
The raw output is the values from Maxent exponential model itself; as such they are not intuitive to work with (Phillips and Dudik 2008). The cumulative output rescales the raw values by applying a percentage to each cell based on the maximum value achieved across the distribution. Thus, the cell with a value of 100 is most suitable and those nearer 0 are least suitable within the study area (Hernandez *et al.* 2006; Phillips *et al.* 2006). The cumulative output does not necessarily represent the probability of presence. For instance a generalist species whose range is represented across the entire study area will have similar probability values across the whole region, slight variations in values will result in big variations in percentages, even though there is little variation in suitability, as a result of their rank from 0 to 100 (Phillips *et al.* 2006). The third output, and the Maxent default, is logistic, it gives a presence probability estimate between 0 and 1, conditioned on the environmental variables (Phillips and Dudik 2008). Low logistic values represent marginal suitability or unsuitable habitat for the species, values near or equal to 1 are highly suitable sites (Phillips and Dudik 2008).

The predicted probability that conditions are suitable are indicated by a colour gradient in the mapped species distribution, where green indicates conditions which have a high affinity with the species requirements, grading to red where there is a low likelihood that the species is present. The output is continuous, as opposed to categorical, so that one can discriminate minor differences in habitat suitability across the region of interest (Phillips *et al.* 2006).

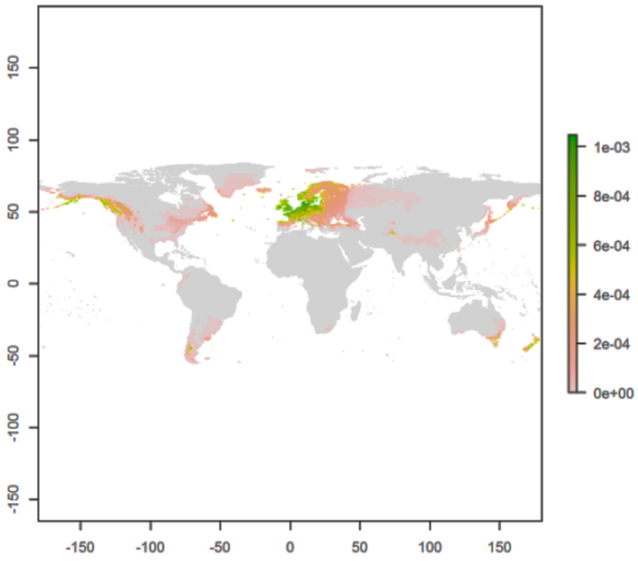
To illustrate the variation across the map output types the Maxent model was run for the Common Frog using the set of eight environmental variables outlined in the Model inputs section (Figure 2 b-d). The distribution of the European Common Frog as predicted by Maxent is shown alongside that of the IUCN recognised current distribution (Kuzmin *et al.* 2012), for comparison. These predictions were created using the set of eight environmental variables, which use is appropriate as there are above 40 unique data points. The distribution predictions are provided in Maxent produced raw format and logistic format, the Maxent default, to illustrate the utility of each. Also included is a map created using a presence-absence threshold, based on the logistic scores; suitable habitat is defined as those grid locations in which a habitat suitability score of 0.5 and above occurs.



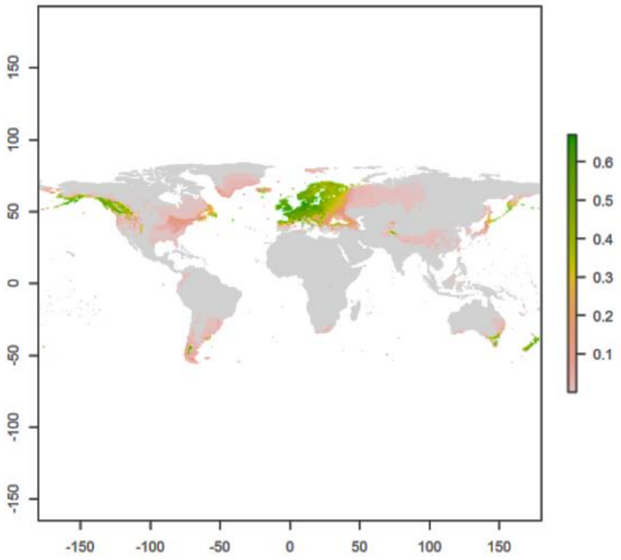
a) Current Distribution



b) Presence-absence map



c) Raw Map



d) Logistic Map

Figure S 2 An illustration of the alternative Maxent Map Outputs using Rana temporaria data, a) Current Distribution (Kuzmin *et al* 2012), b) Projected distribution with threshold applied, c) raw output, d)logistic output

The Maxent prediction, represented in the logistic format, captures the major part of the current range of the European Common Frog Figure S 2d. The model distinguishes the southern barrier of the Pyrenees and the eastern extent of the frog's range in Europe. It also recognises that the area comprising parts of Hungary and Slovakia constitute less suitable habitat. However, it over-predicts the species European range, including areas of southern Italy, and through into northern Turkey beyond which the species actual distribution extends. More crucially, the model is predicting suitable habitat in areas of North and South America and Southern Australia and New Zealand. This is not to say that suitable habitat does not exist in these regions, but that these regions are beyond the natural dispersal range of these frogs.

The presence-absence map (Figure S 2b) is created using a predetermined threshold, where regions of habitat are determined as suitable in grid squares scoring above 0.5 or 50% probability of suitability, thus the threshold defines at what value above which the model classifies a presence and vice versa for an absence (Heikkinen *et al.* 2006). As such regions of suitable habitat appear in green and region outside this suitability threshold in grey. In scaling this predetermined threshold up or down one can alter the extent to which 'suitable' habitat is captured in the model output depending on the use of the final map. For instance, larger thresholds tend to decrease commission errors but increase omission errors (Hernandez *et al.* 2006). Although dichotomous presence-absence classifications are attractive to decision makers they can introduce distortions such as bias (Fielding and Bell 1997), which raises further uncertainty in the final prediction.

In comparing the raw model output (Figure S 2c) and the logistic, the logistic scaling (0 indicates unsuitable habitat and 1 highly suitable) is decidedly clearer, and more easily interpretable. The logistic map makes identifying the core suitable habitat for the species straightforward as highly suitable habitat is clearly indicated in green. The raw output values are fairly meaningless because it represents the initial result of the exponential model and is unstandardized. Although the presence-absence map clearly defines the suitable habitat, this output overshadows the nuances in degree of habitat suitability implicit in the projected distribution.

Statistical analysis

Model Performance

Maxent has several performance measures available to the user, with AUC as the recommended measure (Phillips 2008). For an in depth discussion on performance measures, in particular how AUC is calculated see section 'Threshold Independent Measure: AUC' in Appendix One.

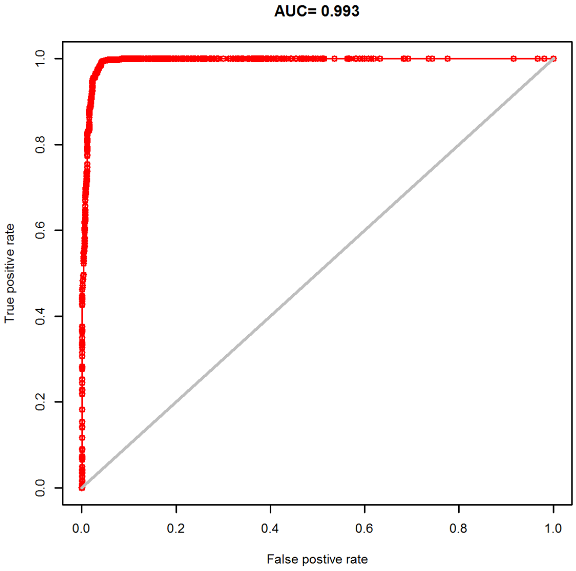


Figure S 3 The Receiver Operating Characteristic Curve created in Maxent using Rana Temporaria

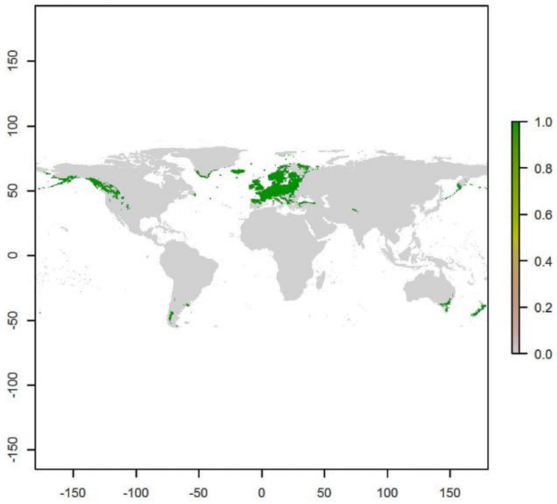
The ROC and AUC corresponding to the prediction for the European Common Frog using eight variables is shown in Figure S 3, and indicates the statistical power of the model in predicting the specie's range. The red line indicates the 'fit' of the model to the data, and reveals the models predictive power, the black line demonstrates that expected if the model was no better than a random model (Phiilis and Dudik 2008). The graphical representation of the model in Figure Three shows that the model is closely mirroring the species requirements defined by the environmental variables, as the curve is above the random model line and is correctly identifying a high proportion of true presences. This indicates that the model's prediction of the habitat suitability niche identifies closely with that defined at the known species presence sites. The AUC score of 0.993 further indicates that the model is accurately predicting suitable habitat for the European Common Frog. This score is potentially inflated in the European Common Frog model because the background data is selected across the entire globe, to further investigate this issue the use of buffers is explored in the section 'the impact of implementing buffers on model accuracy'.

Analysis of the Environmental Variables

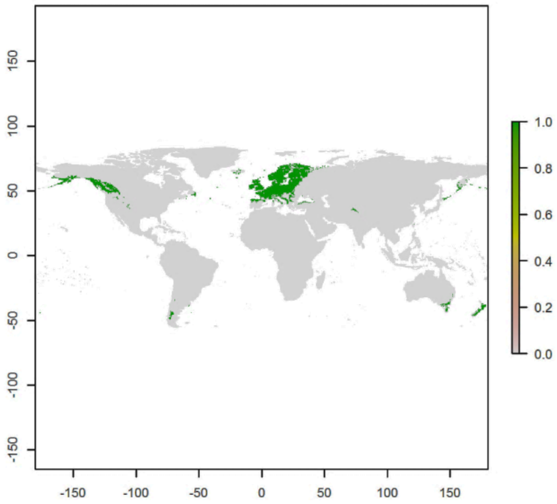
To investigate the effect of, i) varying the number of environmental variables and their geographic resolution, and ii) the suitability of the environmental variables selected in predicting the species of interests climate niche the Common Frog model was run under various different combinations of input variables.

Effect of Varying the Number of Variables

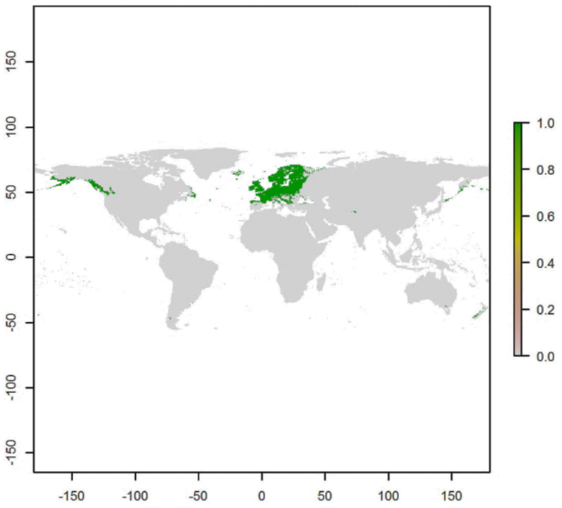
Maxent was run for the Common Frog for each of the three variable sets to examine how the prediction of current distribution and future climate space is affected by varying the number of input variables.



a) 4 Environmental Variables



b) 8 Environmental Variables



c) 19 Environmental Variables

Figure S 4 Presence-absence maps of predictions of Common Frog Distribution under each variable set

Figure S 4 (a-c) shows a comparison of the extent of change in climate space predicted by Maxent for the Common Frog (*Rana temporaria*) using variable sets containing 4, 8 and 19 environmental variables. The resolution is 0.5 degree, equivalent to 50km at the equator. The presence-absence threshold is artificially set at 0.5 for comparison purposes. This comparison illustrates the impact which variable selection may have on output distributions. Visually it is difficult to determine the differences across the three maps, however estimates of current distribution range from 1500km^2 under the 19 variable set to 2100km^2 under the set of four variables, the eight variable set prediction falls between the two predicting a distribution of 1800km^2. Thus, there is a wide disparity between predicted distributions representing the 'current' distribution across the variables sets. The use of fewer variables has been demonstrated to result in larger distributions as the 'representative' environmental niche is less constrained than by the use of 19 variables (Hijmans and Graham 2006). There is inherent risk of overfitting associated with selection of too many variables (Wiens *et al.* 2009). Thus, the use of 19 variables leaves the model prone to over-fitting. These assertions are mirrored in the predictions of the Common Frog for the current distribution in Figure S 4 in which both the four (a) and eight variable (b) set predict a larger distribution extent than the 19 variable set. Under the Wallace Initiative protocol 8 environmental variables would be passed to Maxent for the Common Frog due to the large number of data points.

Exploring Variable suitability

There are several ways to explore which variables most influence a species' distribution in Maxent. During the creation of the projection Maxent tracks the contribution of each variable in fitting the model, and calculates this as a percentage contribution (Phillips 2008). These percentage contributions are subject to the particular algorithm used to create the optimal model, it is possible therefore that different patterns of contribution would produce the same result (Phillips 2008). Maxent also calculates the permutation importance (%) for each variable, which indicates the importance of the variable, modelled in isolation, in predicting presence and background (Phillips 2008 Table S4). Correlation between variables impacts the final values and so caution should be applied when interpreting these data. The contribution of each of the environmental variables in the prediction of the current distribution of the Common Frog under the 8 and 19 variable sets is explored in Table S4 a and b. It is important to note that each variable sets' contributions must sum to 100; therefore these tables cannot be interpreted as a direct comparison of variable contributions. It is therefore only relevant in examining the relative importance of each variable in determining the final species distribution under those particular model conditions. The percent contribution is dependent on the route that the model took in calculating the prediction, thus it is the permutation importance which is of more interest. Permutation importance describes the importance of each variable in the final model and is calculated by randomly permuting the values of that variable across the training points and the model is re-evaluated on the permuted data. It then measures the resultant decrease in training AUC; variables for which a large decrease is indicated are those upon which the model most depends. To aid interpretation these values are then converted to a percentage with high percentages indicating high importance.

Variables	Code	Percent contribution (%)	Permutation importance (%)
Precipitation Seasonality	bio15	16.6	32.3
Precipitation of Wettest Quarter	bio16	23.4	22.7
Max Temperature of Warmest Month	bio5	18.2	14.5
Annual Mean Temperature	bio1	10.2	9.9
Min Temperature of Coldest Month	bio6	1.6	8.7
Precipitation of Driest Month	bio17	9.0	7.9
Annual Mean Precipitation	bio12	21.0	3.5
Temperature Seasonality	bio4	0.1	0.5

a) Variable contributions under the eight variable set

Variables	Code	Percent contribution (%)	Permutation importance (%)
Precipitation of Driest Month	bio14	10.8	42.8
Annual Mean Precipitation	bio12	15.9	10.3
Precipitation of Wettest Month	bio13	5.8	8.5
Mean Diurnal Temperature Range	bio2	12.4	7.8
Annual Temperature Range	bio7	11.4	7.7
Precipitation of Warmest Quarter	bio18	9.5	7.7
Mean Temperature of Wettest Quarter	bio8	0.5	3.6
Mean Temperature of Coldest Quarter	bio11	0.1	2.2
Annual Mean Temperature	bio1	1.4	1.9
Precipitation Seasonality	bio15	3.0	1.5
Mean Temperature Driest Quarter	bio9	0.0	1.5
Mean Temperature of Warmest Quarter	bio10	0.3	1.4
Precipitation of Coldest Quarter	bio19	0.1	1.2
Min Temperature of Coldest month	bio6	18.3	0.6
Max Temperature of Warmest Month	bio5	0.1	0.6
Precipitation of Driest Quarter	bio17	6.0	0.2
Precipitation of Wettest Quarter	bio16	0.3	0.2
Isothermality	bio3	5.1	0.1
Temperature Seasonality	bio4	0.0	0.0

b) Variable contributions under the 19 variable set

Table S 4 Contribution of each variable to the prediction of the Common Frog's current distribution Purple shading illustrates variables included in the four and eight variable to aid comparison..

Bio1 to Bio11 represent different measures of temperature and Bio12 to Bio19 represent precipitation measures. The 8 variable subset variables are balanced representing 4 temperature-based (bio1, bio5, bio6, bio4) and 4 precipitation-based (bio12, bio15, bio16, bio17) measures.

The top 3 ranked variables within the set of 19 are all variables representing precipitation measures. As the species in question, *Rana temporaria* is a frog species associated with aquatic habits, relying on water bodies to breed (Kuzmin *et al.* 2012), this result would be expected. The top two ranked variables in the subset of 8 are also precipitation measures. Only one of the 8 variable subset variables appear in the top ranked eight variables in the full suite of 19 variables, annual precipitation (bio12). In essence the model with 19 variables ranked seven variables above those selected within the 8 variable subset. However, this calculation does not take into account correlation between the variables; multicollinearity doesn't impact model accuracy but can influence calculations regarding individual predictors. In both cases there are two variables which explain over 50% of the niche space. For the 8 variable subset these variables (bio15 precipitation seasonality and bio16, precipitation driest quarter) explain 55% of the variation and in the suite of all 19 the two variables (bio14 precipitation driest month and bio12, annual mean precipitation) explain 53.1%. Although these most influential variables do not match across the variable sets there are similarities between them, insofar as they are all precipitation-based and include measures over dry periods. In this case the Wallace Initiative 8 variable set does not contain all those variables best suited in calculating the Common Frog's climate niches however, one needs to bear in mind the 8 variables selected by the Wallace Initiative were selected on the basis that they can be extrapolated across a broad range of species, including mammals, birds and reptiles.

The Impact of Environmental Variable Resolution on Predictions

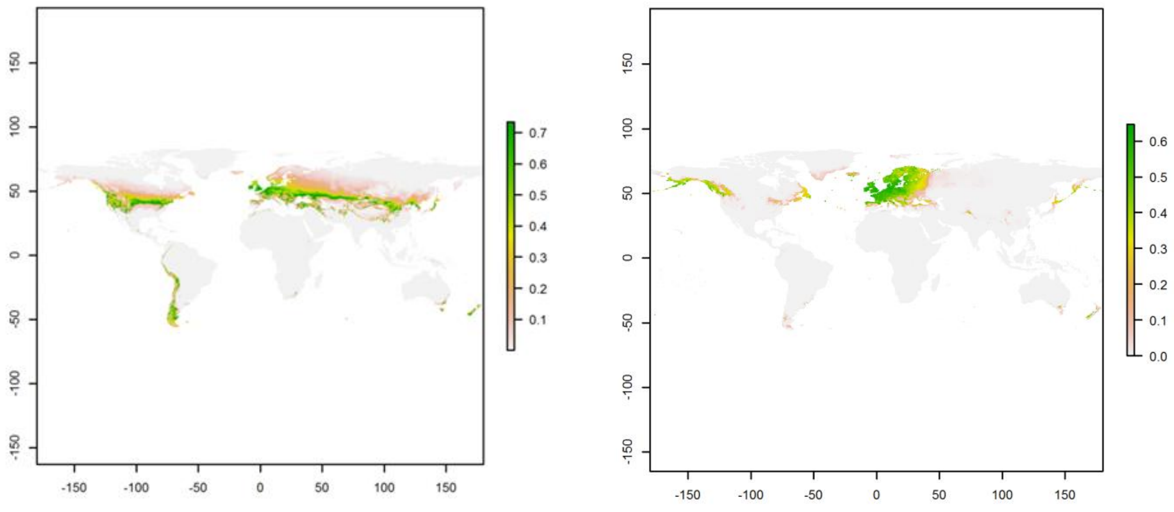
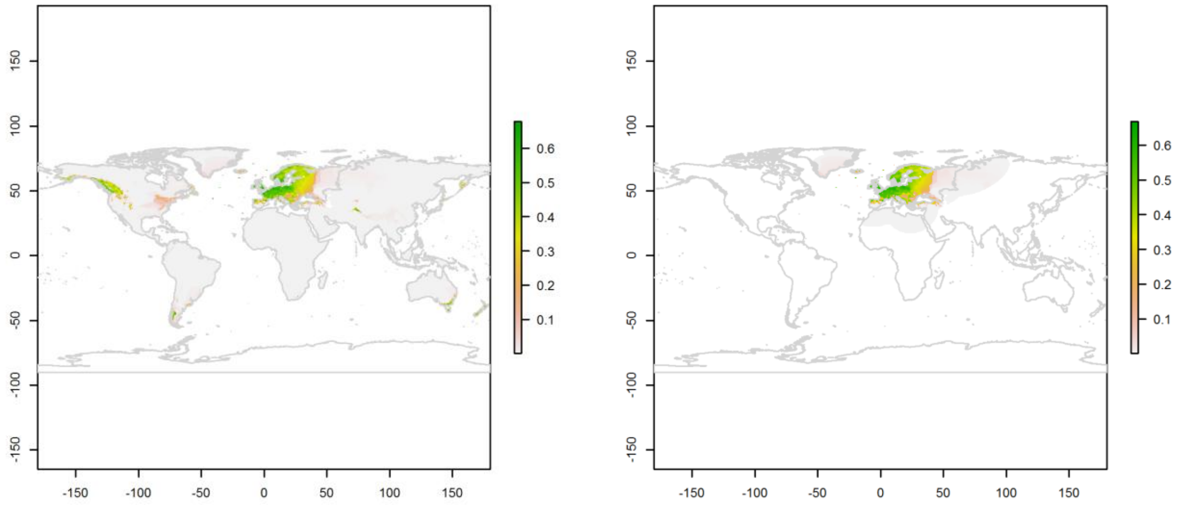


Figure S 5 Demonstrating how the resolution of environmental variables impacts Maxent's ability to determine a species environmental requirement. Left: High resolution (10 arc-minutes), Right: Low Resolution (0.5°x0.5°).

To investigate the impact of resolution on predictions of climate niche the Common Frog's climate niche was recalculated for two different resolutions using Maxent

((Figure S 5). These maps illustrate how the resolution of the environmental variables impacts the models ability to infer the species niche envelope. The high resolution data is a 10 arc-minute projection equivalent to 18.6km^2 area at the equator; the low resolution data is 0.5°x0.5° grid cells or 50km^2 at the equator. The prediction created using high resolution data predicts a wider distribution. The likely reason for this difference is that the model picked up nuances in the environmental data represented by the occurrence points that have been masked by the coarser scale of the low resolution grid (Elith *et al.* 2011)

The Impact of Implementing a Buffer on Model Predictions



a) b)

Figure S 6 Demonstration of the application of the buffer in constraining the projection a) non-buffered, b) 2000km buffer

To examine the impact of implementing a buffer the eight variable model for the Common Frog was re-run with an additional file in which the buffer is described (Figure S 6). The application of a buffer bounds the species projected distribution by the restriction of the model prediction to only subset of the entire region. The buffer used in this case reflects that used in the Wallace Initiative at a 2000km distance around the occurrence points (Figure S 6b). The light grey shading demarcates the area over which the model is projected. The buffer goes someway to preventing species projections ‘colonizing’ areas which represent similar environmental characteristics but are outside the reach of the species current distribution Figure S 6a. The Common Frog’s distribution in reality lies squarely in the European Palaearctic; however, without the buffer it is erroneously predicted to reside in North Americas.

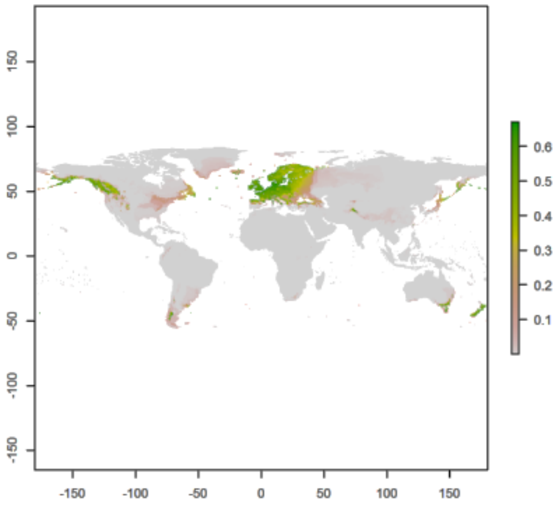
Creating Future Projections of Species Distributions

The projection of species distributions into the future requires two sets of environmental data, representing, i) the current conditions, onto which the modelled distribution is trained, and, ii) future predicted conditions under climate change, onto which the climate niche requirements are projected to create a map of future climate suitability. These variable sets must be of the same extent and resolution for the model to run. Projections of the Common Frog's future climate space were created to investigate the impact of future climate change on the species distribution and the effect of altering the number of input variables on future projections.

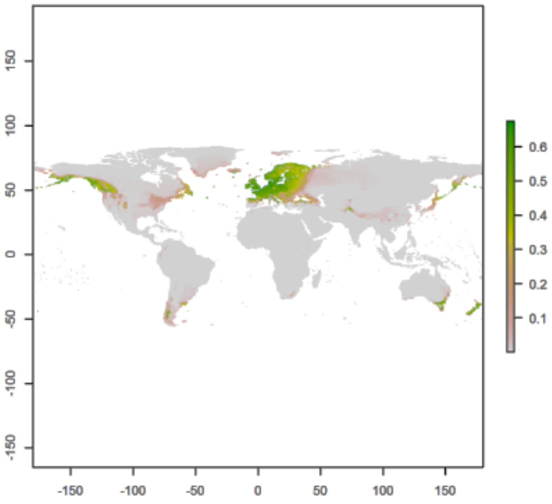
Future projections of species distribution are made using the global warming scenario 'SRES A1B' as defined in the IPCC AR4 report (Solomon *et al.* 2007). The 'SRES A1B' (Pachauri and Reisinger 2007) storyline describes a world of rapid economic growth, where the global population peaks mid-century and there is rapid introduction of more efficient technologies. This scenario represents a temperature increase of 2.8°C (1.7°C-4.4°C) by 2090-2099 relative to the temperature at 1990-1999 (Pachauri and Reisinger 2007).

The projected changing climate suitability for the Common Frog under climate change is illustrated across the period 2020-2080 in Figure S 7a-d. These mapped projections were created using the eight variable set. In these projections the Common Frog's distribution appears fairly stable over the period in a comparison with the current predicted range, with only small changes in the extent and degree of suitability observable. For instance, in the projection for 2080, although the extent of the distribution shows little change from 2050, climate suitability increases slightly in the eastern region of the distribution. This observation is further reflected in the increase in distribution in 2080 apparent in Figure S 7d, which represents total land area in which climate suitability exceeds the 0.5 suitability threshold.

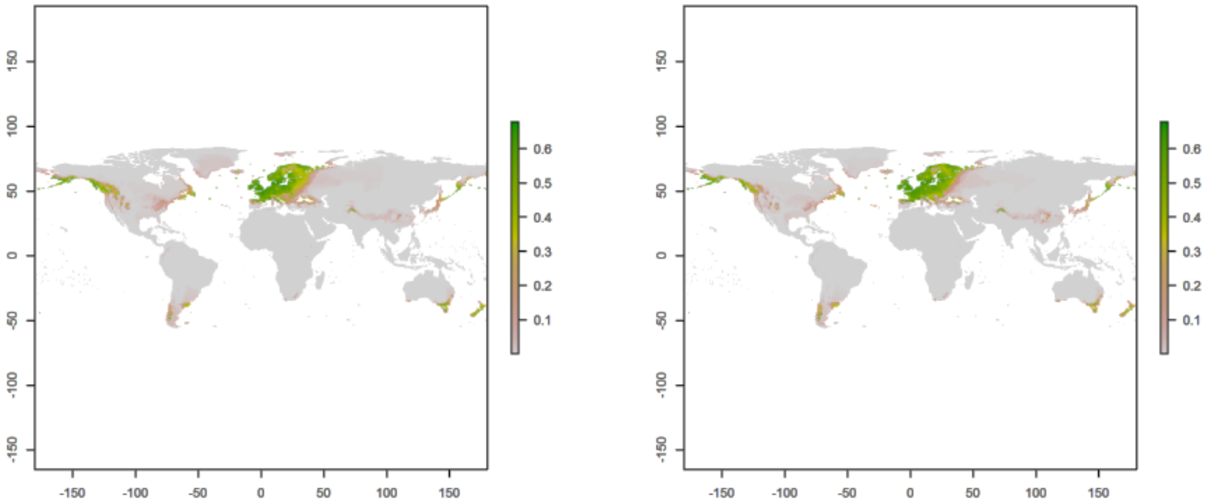
Figure S 7e is a comparison of the climate niche extents predicted by each of the variable sets from current to 2080. There is wide variation across the three sets of variables across the period. The four variable suite projects the greatest extent of climate space for the Common Frog under current conditions, with the suite of 19 projecting the least extent. However, beyond 2020 and to 2080, it is the eight variable suite which projects the largest extent of climate space. The four variable suite projects a sharp decline in suitable climate space whereas the nineteen variable suite predicts the suitable climate space to remain relatively stable at 2020. Beyond this point both variable sets predict a slight rise in suitable climate space to 2050 and then a decline to 2080. The sharp decrease in the extent of suitable climate space projected by the four variable set to 2020 is likely to be related to the fact that they are no longer able to accurately predict the species niche under future conditions because the model fails to take into account the nuances in the species climate niche. Therefore, we can discount the four variable set for the projection of the Common Frog's future suitable climate niche.



a) Current distribution

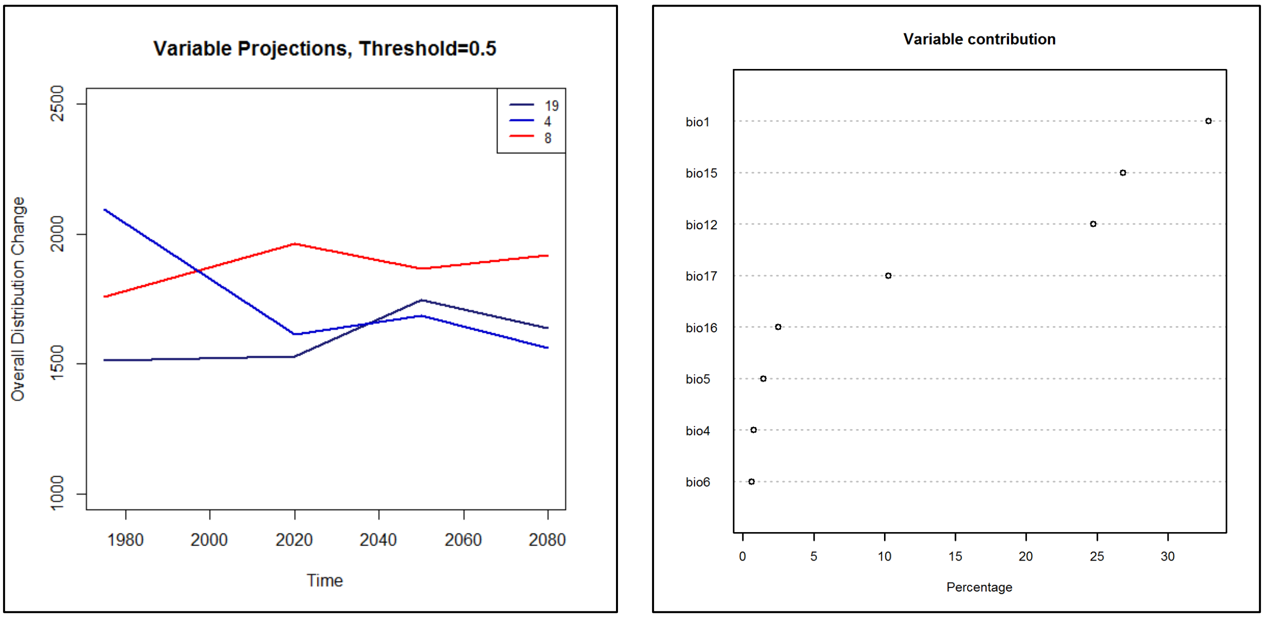


b) 2020



c) 2050

d) 2080



e) Distribution Change by Variable Set

f) Variable contribution under the eight variable set

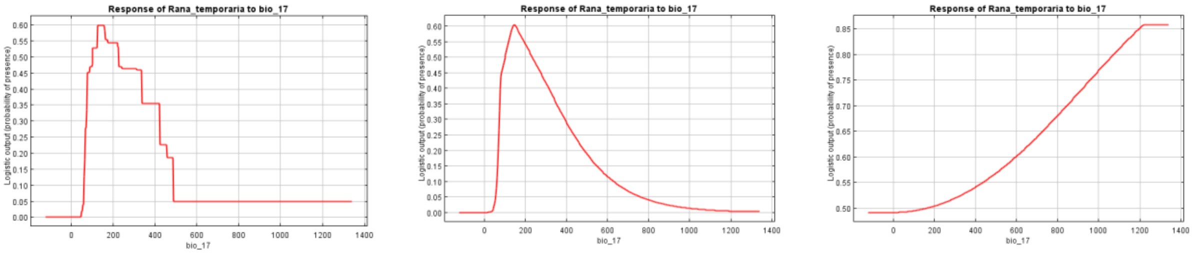
Figure S 7 Future Projections created under the SRES A1B scenario for the eight variable set a) current, b) 2020, c) 2050, d) 2080, and e) Comparison of projected extent of suitable climate under 4, 8 and 19 variable set, f) Variable contributions under the 8 variables

In a comparison across the variable contributions created under the current conditions and future scenarios (Figure S 7e), those variables which most contributed to the final predictions change over time. For instance, the projection created under current conditions is driven by mean precipitation in the wettest quarter (bio16), annual mean precipitation (bio12) and maximum temperature of the warmest month (bio5). Under the scenario of future climate change, annual mean temperature (bio1) and precipitation (bio12) and precipitation seasonality (bio15) are the major drivers. The increasing influence of mean annual temperature in describing the habitat conditions suitable for the Common Frog into the future may indicate that increasing temperature becomes a limiting factor into the future.

Investigating Model Settings

Feature types & their associated response curves

There are six feature types which support the Maxent algorithm in its calculation of species distributions, these are the: linear feature; hinge feature; quadratic feature; product feature; threshold feature and category indicator feature (Phillips and Dudik 2008). The 'feature types' control the way in which the Features (input variables) are weighted. Five of the six feature types are derived from continuous variables, the exception being the category indicator feature which is derived from categorical variables (Phillips and Dudik 2008). To illustrate the effect of varying the features used when implementing the model response curves were created for comparison, these were generated using the Common Frog data and the eight variable set. Maxent automatically selects the features which are most appropriate for the data (Phillips and Dudik 2008). The linear feature is always used, the quadratic feature only in circumstances when there are 10 records and above, the hinge feature requires 15 records to run and the threshold feature at least 80 records (Elith *et al.* 2011). This is because the fewer records available the greater the difficulty in determining a relationship between species occurrences and environment so the model is required to be less statistically complex (Pearson 2007a; Elith *et al.* 2011). The linear, quadratic and product features constrain means, variances and covariance of the continuous variables, respectively, when matching their empirical values (Phillips and Dudik 2008). The 'threshold' feature is a binary function which sets a threshold value, v, assigning the value 1 where the environmental variable has a value exceeding the threshold and 0 if the value is below the threshold (Phillips 2008). The threshold feature has the effect of making the 'total probability of grid cells with a value greater than the threshold equal to the fraction of sample locations with the value above the threshold' (Phillips 2008) . The hinge feature is similar to a linear function, derived from continuous environmental variables, it is constant below the threshold, *v* (Phillips 2008). Selecting the 'Threshold' feature type result in step-like response curves because they are a form of step-function (Phillips 2008). The Maxent output is created by summing the features, thus, summing the threshold features will always result in a step function, hinge-only features result in a piece-wise linear exponent , which is visualised graphically as a series of straight-line sections (Phillips 2008) .



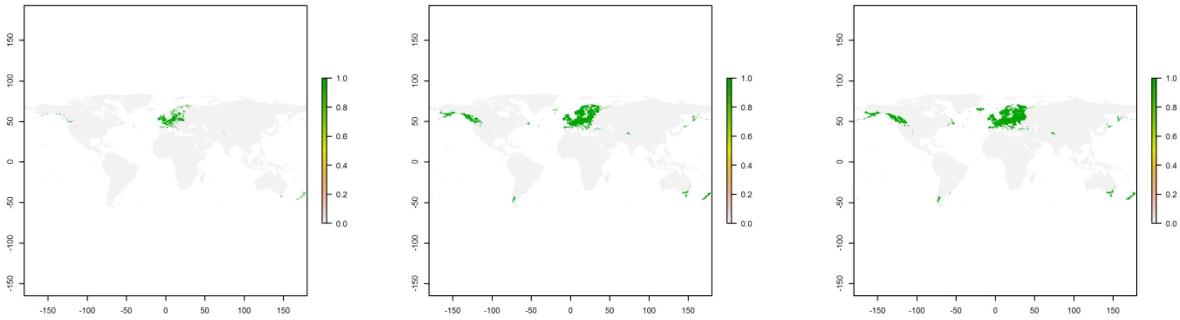
a)Threshold b) Hinge c) Quadratic

Figure S 8 Illustrating the effect of feature types on model response curves

As can be seen in Figure S 8, which illustrates the response curves for the Common Frog, using the threshold feature creates a stepped response curve, whereas using the hinge and quadratic features the curve is smoothed. In their 2011 paper Elith *et al* found that running subsets of feature types has the effect of simplifying the model. Running the model with the hinge feature but not the threshold function leads to a less complex smoothed model (Elith *et al.* 2011). Excluding the product feature the model becomes easier to interpret although less able to model complexities in the relationship between species occurrences and environmental variables (Elith *et al.* 2011). Phillips & Dudik (2008) recommend using Maxent's default settings because tuning the parameters of the model to each species is time-consuming, justification of the defaults use can be validated by their repeated use over a wide range of species, environmental variables, sample size, and different degrees of sample selection bias.

The Regularization setting

Use of maximum entropy has been found prone to overfitting (Phillips and Dudik 2008). Thus, in Maxent the developers employ regularization, a form of relaxation which forces the model to account for values close to the average value of a predictor rather than equal to it when estimating the distribution (Phillips *et al.* 2006). The degree of regularisation varies flexibly to account for sample size to ensure a consistent performance (Phillips *et al.* 2006); a larger regularization multiplier will result in a less-localised, more spread out prediction (Phillips *et al.* 2006). The type of regularization employed also tends to reduce the number of variables in the model by omitting irrelevant variables, reducing the variance but potentially upping the bias (Wisz *et al.* 2008). Balancing these two factors correctly will result in model that is most parsimonious and that is best able to predict unseen observations (Wisz *et al.* 2008).



a) Regularization=0.01
AUC= 0.989

b) Regularization=1
AUC=0.991

c) Regularization=5
AUC=0.922

Figure S 9 Demonstration of the effect of altering the Regularization multiplier on the model projection

To illustrate the effect of implementing the regularization multiplier the Common Frog model was re-run using different levels of regularization under the eight variable set. Figure S 9a) represents a regularization value of 0.01, the resulting distribution is extremely localised to the occurrence points. This has the effect of restricting the models ability to generalize well to independent testing data, the data is thus overfit. Figure S 9b) represents the Maxent default model where the multiplier equals 1 for comparison. The distribution created using a regularization multiplier of 5 (Figure S 9c) is more diffuse than those in S 9a) and S 9b) in a less localised prediction. However, too large a multiplier impacts the model’s parsimony and may lead to underfitting, where the model is unable to determine well suitable habitats using testing data as the species niche is too loosely-bounded.

Conclusion

The exploration into the alternative ways of running of Maxent in this case-study of the Common Frog has helped to elucidate upon the most appropriate way of running Maxent to create current and future projections of species distributions. It has also served to explore some of the reasoning behind the methods used in creating the projections created in the Wallace Initiative upon which the wider study is based.

In regards to the most appropriate way of running Maxent for a single species, this study would recommend the following approach:

- Prepare the input occurrence data to remove wrongly geographically referenced and duplicate occurrences.
- Run the Maxent default model as Maxent automatically selects the most suitable feature types for the data.
- Where there are 40+ occurrence points initially run the model with the full suites of environmental variables to determine the species environmental niche using bootstrapping and the permutation tables. Then re-run with the top most influential variables identified by bootstrapping to avoid overfitting.
- Use high resolution environmental data in the creation of current predictions to identify the largest range of variation within the species environmental niche.
- Create upwards of 10 replicates to reduce uncertainty within the predictions.
- Limit the region within which the model searches for appropriate climate space using a buffer so that predictions are constrained within the likely extent of the species. Restricting the spatial extent over which the model can predict the species current distribution reduces the risk of overfitting, whilst also stopping the species being predicted outside the species historical extent (Anderson and Raza 2010). A too restrictive buffer will prevent the model from identifying climatically suitable regions which are not represented by the species occurrence data causing a deflation in the prediction of current extent. Therefore, it has been suggested that the buffer be determined based on the recent historical extent of the species (Hortal *et al.* 2012).
- Use the log format mapped predictions rather than presence-absence maps to avoid masking potential suitable climate space.

When running an automated model with a broadly ranging suite of species, the case in the Wallace Initiative (Warren *et al.* 2013) the mechanism by which Maxent determines the most appropriate environmental variables cannot be automated. Therefore a set of environmental variables judged to be salient in determining a wide-range of different species climatic requirements must be defined *a priori* based on the literature. This is also the case when determining a suitable buffer in the Wallace Initiative analysis (Warren *et al.* 2013) the buffer restricts species distribution shifts to within a 2000km radius and to remain within the continent in which they currently occur. The Maxent model is extremely useful in creating predictions of current and future projections under climate change for conservation studies. However, care must be taken to select the most appropriate inputs to maximise the usefulness of the outputs. One should also be aware of the caveats associated with environmental niche models in general and acknowledge these when presenting results (See Appendix on Model Appraisal for further details).

Appendix 3: Visualising Climate Change: Examining Uncertainty in GGM projections of future climate change

Maxent requires the input of projected future climate in the shape of environmental variables. These environmental variables are created using climate patterns projected by a General circulation model (GCM). The employment of GCMs in providing these projections requires understanding of the uncertainties, strengths and weaknesses associated with GCMs. This appendix seeks to explore the uncertainty associated with GCMs, and how each corresponds or differs in their individual projections of future climate change. Further, it seeks to explore the impact of this uncertainty on the prediction of species' future climate space.

Introduction

Confidence in the ability of climate models to project future climate change is considerable particularly at the continental scale and above (IPCC 2007). This confidence is rooted in the underpinning of the models in well understood physical principles and their ability to replicate patterns of past and current climate changes (IPCC 2007). These mathematically- represented physical laws include the conservation of mass, energy and momentum and are supported by a vast number of observations (IPCC 2007).

However, in predicting climate into the future there is recognised uncertainty associated with the GCMs used to model the projections (Beaumont *et al.* 2008). There is no one 'best' model (Beaumont *et al.* 2008). Variation in predictions of future climate are associated with the method in which climate is represented statistically in the model (Beaumont *et al.* 2008). For instance, the accurate representation and parameterization of some physical processes, such as soil moisture, is especially difficult (Beaumont *et al.* 2008). Imperfect understanding relating to climate sensitivity to changes in greenhouse gas concentrations also introduces considerable uncertainty (Beaumont *et al.* 2008). Uncertainty is also associated with the models ability to project small-scale climate process such as tropical precipitation, the El Niño-Southern Oscillation and the Madden-Julian Oscillation (a short-lived (30-90 days) variation in tropical rainfall and winds) (IPCC 2007). This uncertainty is both related to scientific understanding of these smaller scale climate mechanisms but also computing power (IPCC 2007). Mountainous areas and areas of coastline particularly also complicate the prediction of future climate as they have significant impacts on localised micro-climatic patterns (Rajib and Rahman 2012). The impact of this related uncertainty is dependent on the application of the model, however all climate models project global-scale warming as a result of increased greenhouse gases (Meehl *et al.* 2007).

The use of a single climate realisation in projecting future species distributions has the potential to misrepresent future species exposure to climate change (Beaumont *et al.* 2008). This is because by projecting a species future niche onto a single climate projection one is sampling an unknown fraction of possible future conditions (Beaumont *et al.* 2008). In using an ensemble of climate models in the projection of future species distributions, as shown in this appendix, one can minimise this source of uncertainty.

To reduce the uncertainty associated with species distribution model outputs the selection of appropriate GCMs and understanding their attendant uncertainties is an important step (Beaumont *et al.* 2008). The climate patterns of seven GCMs are utilised in the creation of projections of species future suitable climate spaces in this study. The seven GCMs are the UKMO-HadCM3, CCCMA-CGCM3.1, IPSL-CM4, MPI-ECHAM5, UKMO-HadGEM1, CSIRO-Mk3.0, and NCAR-CCSM3.0 and were created using CLIMGEN a model for generating pattern-scaled climate data (Warren *et al.* 2013). This appendix specifically examines patterns of mean annual temperature and mean annual precipitation at 2080. The climate data visualised in this appendix were extracted from the Wallace Initiative website (Wallace Initiative 2013).

Current Climate

To provide a basis from which to compare future projections of climate the current observed mean annual temperature and mean annual precipitation are also included. Current climate maps are derived from observations of annual mean temperature and annual mean precipitation between the period 1961-1990, data available on the Wallace Initiative website (Wallace Initiative 2013).

Mean Temperature

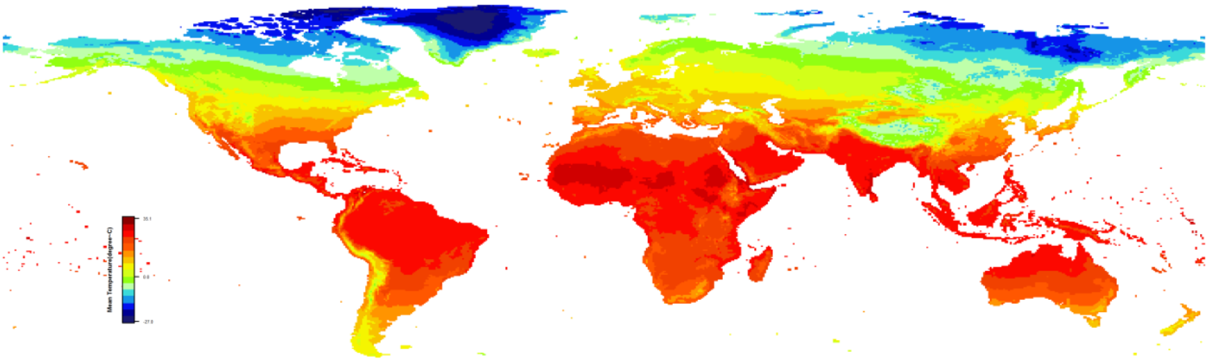


Figure S 10 Global Annual Mean Temperature (1961-1990, °C)

The observed global annual mean temperature range is -27.8°C to 30.4°C (Figure S 10).

Mean Precipitation

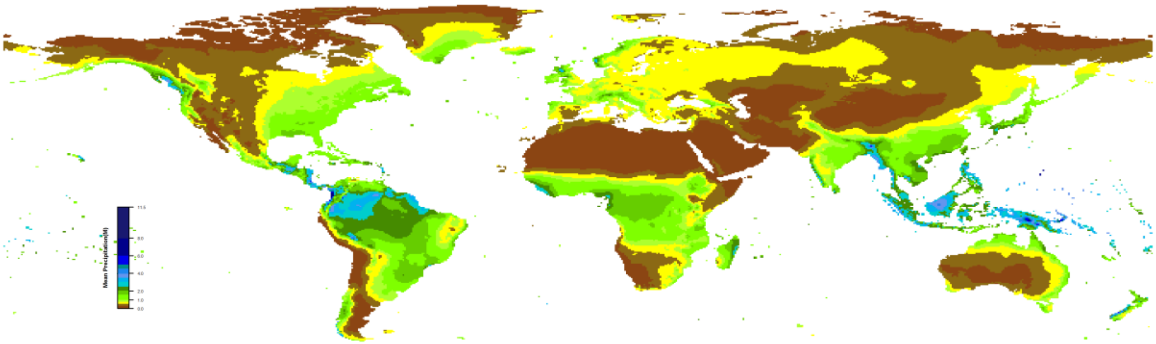


Figure S 11 Current Annual Mean Precipitation (1961-1990 (m/yr))

Observed mean annual precipitation across the period 1961-1990 ranged between 0-7.6 m/yr (Figure S 11), (Wallace Initiative 2013). The driest areas are indicated in brown moving through to dark blue for the wettest areas. The wettest areas are observed in the Southern Hemisphere in the Amazon basin and across Indonesia and the Philippines. The driest areas are in Northern Africa and the Middle East, central Australia and across the Himalayas and the Arctic Circle.

Exploring Future Mean Annual Temperature and Precipitation Projections

The GCMs used in this Study

The following projections of annual mean temperature and annual mean precipitation were created for each of the seven GCMs under the SRES A1B scenario to 2080 (Table S 5).

	Mean Annual Temperature (°C)		**Mean Annual Precipitation (m)**	
GCM	**Minimum**	**Maximum**	**Minimum**	**Maximum**
Observed climate	-27.8	30.4	0	7.6
cccma_cgcm31	-23.3	35.6	0	8.5
csiro_mk30	-23.2	35.1	0	9.8
ipsl_cm4	-22.9	34.7	0	10.0
mpi_echam5	-22.9	35.1	0	8.6
ncar_ccsm30	-22.9	34.3	0	10.2
ukmo_hadcm3	-22.8	35.1	0	11.5
ukmo_hadgem1	-22.6	34.0	0	9.9
Mean	-22.9	34.9	0	9.7

Table S 5 Comparison of annual mean temperature and precipitation by GCM at 2080 with observed climate.

The GCM ukmo_hadgem1 predicts the lowest global minimum temperature and maximum temperature at 2080. The GCM which predicts the highest minimum and maximum temperature at 2080 is ccma_cgcm31 at -23.3°C and 35.6°C, respectively. Thus, between the two GCMs there is predicted a 0.7°C difference in minimum mean annual temperature and a 1.6°C difference in maximum annual temperature by 2080. To minimise uncertainty the Wallace Initiative calculates the mean value of annual mean temperature by removing the minimum and maximum extreme values and takes the average over the remaining five GCMs (Warren *et al.* 2013). Using this method the mean of the GCMs for minimum mean annual temperature is -22.9°C and the maximum is 34.9°C. When comparing future predicted mean annual temperature to the observed temperature there is an average 4.9°C (4.6°C- 5.2°C) predicted rise above the minimum mean annual temperature from current to 2080. There is predicted an average rise of

4.5°C (3.6°C-5.2°C) between the observed maximum mean annual temperature and that projected at 2080.

Minimum annual mean precipitation is 0m across the full set of GCMs and current observed precipitation values. The GCM cccma_cgcm31 predicts the lowest maximum value for mean annual precipitation at 2080 at 8.5m; the highest is predicted by the GCM ukmo_hadcm3 at 11.5m by 2080. The average value of maximum annual mean precipitation across the GCMs is 9.7m; this represents a rise of 2.1m (0.9m - 3.9m) above the current observed value at 7.6m by 2080.

Future Temperature by GCM

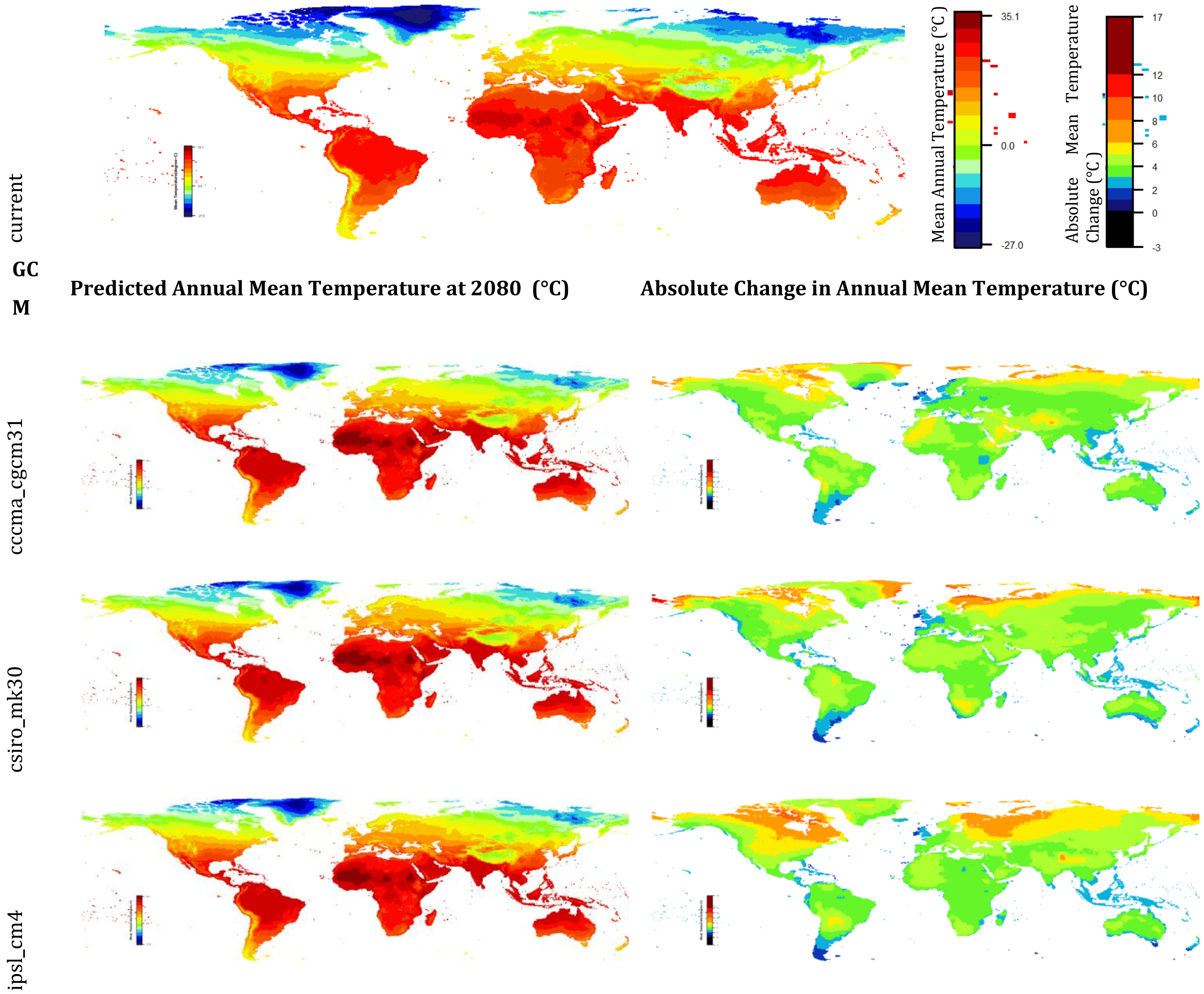
This section analyses the variations across GCMs in their projections of Annual Mean Temperature under the SRES A1B scenario. Due to understanding of the physical methods by which temperature changes are determined and subsequently statistically represented in climate models variation in temperature across the GCMs is narrower than that for precipitation (IPCC 2007).

Across the GCMs the Sahara region of North Africa is predicted to experience the hottest mean annual temperatures by 2080 with projected temperatures of between 32-35°C this is consistent with the fact that under current climate this area is the hottest with a mean annual temperature of between 28-32°C (Figure S 12). The lowest temperatures are observable in central Greenland across both the current climate and the multiple GCM projections ranging between -27°C to -23°C under current conditions and -23°C and -19°C under future conditions.

Figure S 12 includes a series of Absolute change in temperature maps which illustrate the change in mean annual temperature in degrees Celsius (°C) projected by each GCM from current observed mean annual temperature (1961-1990). The range of projected temperature change is between a 0°C and 17°C increase in temperatures at 2080 from current. Across the GCMs there are no regions where mean annual temperature is projected to remain stable to 2080 with the majority of regions experiencing a rise in temperature of between 3 -6°C above current temperatures.

The region in which the largest temperature increases are projected, with GCMs projecting between a 5°C and 12°C increase in mean annual temperature are within the

North Hemisphere across the Arctic Circle. The regions predicted to experience the smallest degree of absolute warming in mean annual temperature, between 1°C and up to 3°C is less clear cut with a greater degree of variation across the GCMs. However, the GCMs show agreement that absolute temperature increase in the United Kingdom and the Southern tip of South America are likely to be constrained within an increase of 1-3°C.



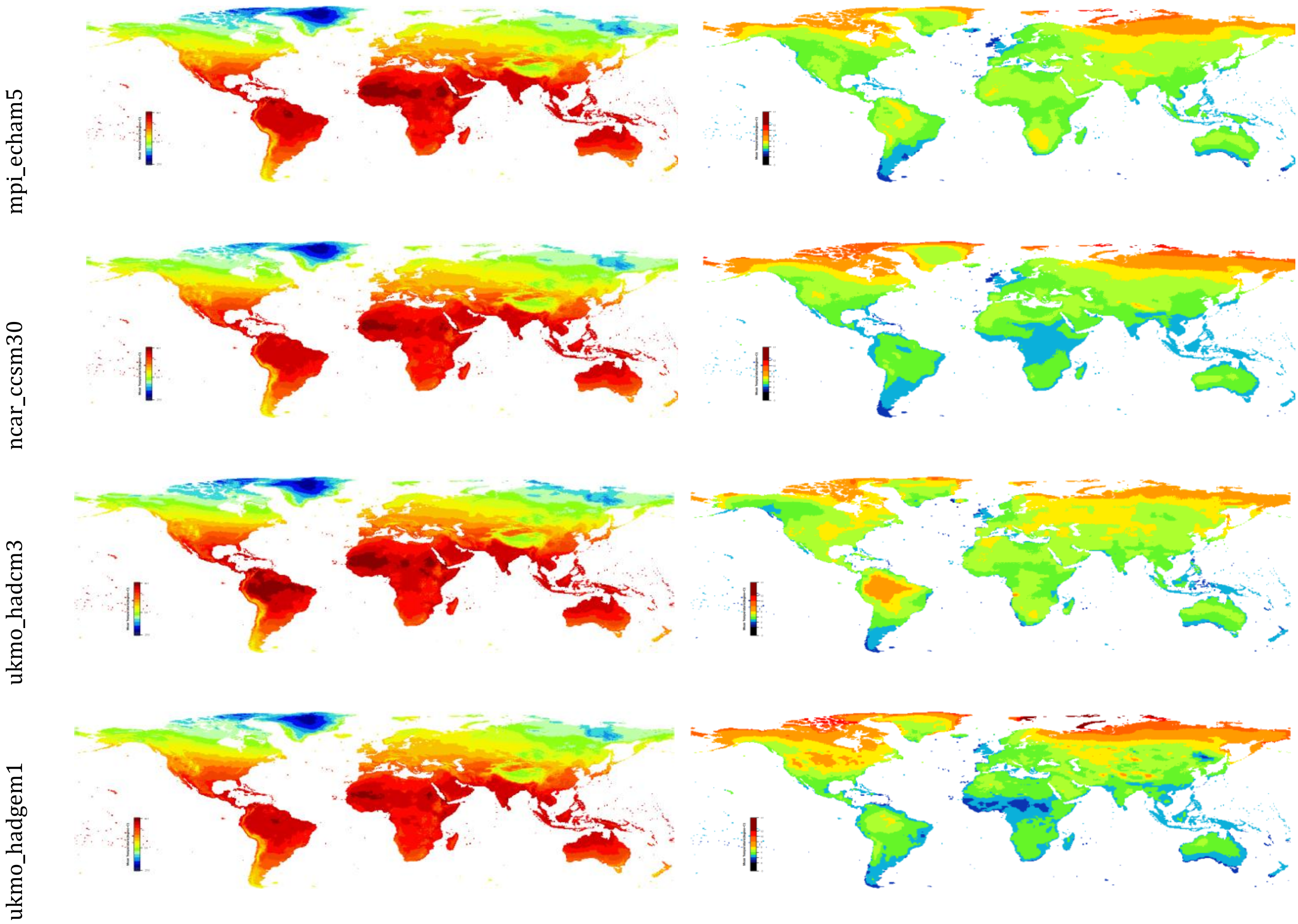


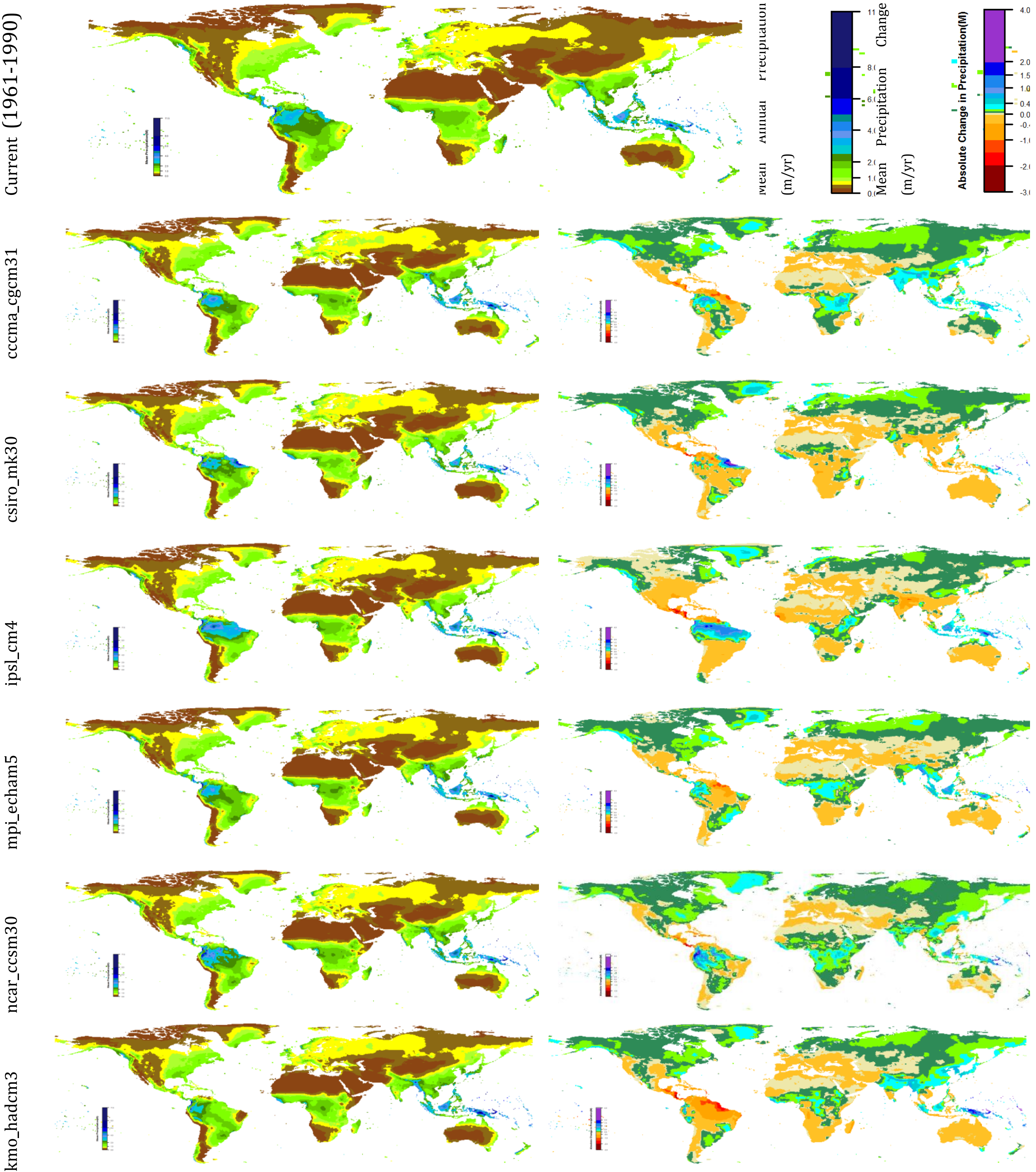
Figure S 12 Maps of the Annual Mean Temperature and Absolute Change in Temperature under the SRESA1B scenario by GCM (2080 AD)

The regions in which the greatest variation is apparent across the GCMs are the tropical regions of equatorial Africa and the Amazon basin in South America. A closer investigation of the equatorial African region shows model projections predicting a rise of absolute temperature to 2080 of between 1-5°C. The smallest degree of absolute increase in temperature is predicted by the GCM ukmo_hadgem1 with a 1-3°C increase across the region. Whereas, the ukmo_hadcm3 GCM predicts an absolute rise in temperature of between 3-5°C. The majority of the remaining models predictions are more closely identifiable with the ukmo_hadcm3 predictions apart from the ncar_ccsm30 which projects a 2-3°C increase. A similar pattern is observable across the Amazon basin, although the hot and cool GCMs, those which predict the largest and smallest annual mean temperature increase from current to 2080 are not consistent with those for the Equatorial African tropics. Projections of absolute temperature change in the Amazon basin vary considerably across the GCMs and ranges between an increases of 2°C up to 8°C. The hottest model is again the ukmo_hadcm3 which projects that a large expanse of the Amazon basin will experience an absolute increase in temperature of between 6-8°C. The ncar_ccsm30 is the GCM with the coolest projection predicting absolute rise in temperature of between 3-4°C across the majority of the Amazon basin. The remaining GCM projections for the Amazon basin predict an average increase of between 4-5°C.

Future Precipitation by GCM

There is greater uncertainty associated with the projection of precipitation than temperature changes due to gaps in scientific knowledge of the driving processes, particularly smaller scale climate mechanisms such as those associated with tropical precipitation (IPCC 2007). This section compares the seven GCMs projections of future change in precipitation comparing both Annual Mean Precipitation and absolute change in Annual Mean Precipitation.

Figure S 13 illustrates maps for both Annual Mean Precipitation (m/yr) and Absolute change in Precipitation (m/yr) to 2080 under the SRES scenario for the full suite of GCMs. The GCMs are consistent in projecting the driest regions of the Earth surface at 2080. The lowest rates of annual mean precipitation, 0-0.25m/yr, are projected at 2080 for large areas of the globe particularly within the Saharo-Arabian region and the western coast of southern Africa, the Northern-most reaches of North America, the Central desert of Australia and across the Andes mountains in South American. The GCMs reliably project that the wettest regions will remain the Amazon basin, the Indonesian islands and the Philippines with annual mean precipitation of between 3-8m/yr by the 2080s.


Current (1961-1990)
cccma_cgcm31
csiro_mk30
ipsl_cm4
mpi_echam5
ncar_ccsm30
ukmo_hadcm3
Mean Annual Precipitation (m/yr)
11
8.
6.
4.
2.
1.
0.
Mean Precipitation Change (m/yr)
Absolute Change in Precipitation(M)
4.0
2.0
1.5
1.0
0.4
0.0
-0.
-1.
-2.
-3.

ukmo_hadgem1

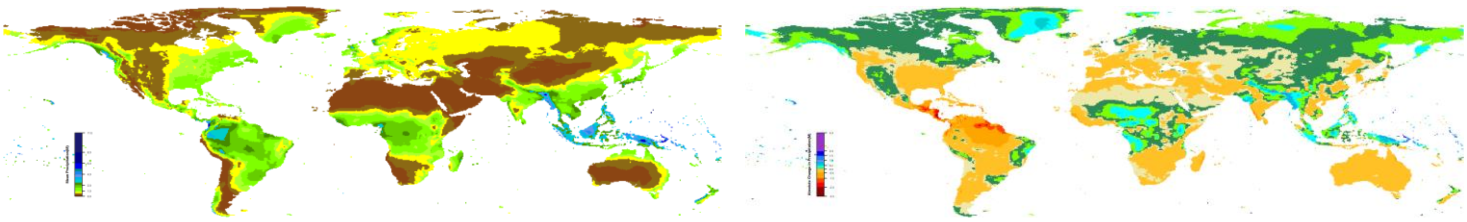


Figure S 13 Annual Mean Precipitation and Absolute Change in Precipitation Maps under the SRESA1B scenario by GCM to 2080

Figure S 13includes a series of Absolute change in precipitation maps which illustrate the change in annual mean precipitation in metres (m) projected by each GCM based on current observed annual mean precipitation (1961-1990). The range of projected precipitation change is between a reduction in precipitation of up to 3m/yr and an increase in precipitation of up to 4m/yr, although the dry extreme is rare within the projections and it more akin to -1.5 to -2m/yr by 2080.

Across the GCMs there are several regions where mean annual precipitation is projected to remain stable to 2080. These areas are indicated in the legend by a buff colour and encompass changes in precipitation of between -0.02m/yr and 0.02m/yr from current to 2080. The region which is determined to remain stable across the full of suite of GCMs is the region encompassing the Sahara desert in North Africa. Areas of central Asia are also determined by several models to retain relatively stable precipitation levels across the period to 2080. However, both regions have already been identified as being within the band of least precipitation with between 0-0.25m/yr.

The regions in which the largest degree of drying are projected are in Central and South America, specifically several GCMs predict drying along the length of Panama and the North-Eastern coast of Brazil of between 1.5-2m/yr less rainfall by 2080. The region predicted to experience the largest degree of additional precipitation are the Indonesian Islands and the Philippines although there is uncertainty across the GCMs as to how much precipitation levels will rise, with predictions encompassing a degree of drying to up to 0.4m/yr to an increase of precipitation up to 2m/yr.

The regions in which the greatest variation is apparent across the GCMs are the tropical region of Equatorial Africa, the Amazon basin in South America and across South-East Asia. A closer investigation of the Equatorial African region shows model projections predicting changes in precipitation from a reduction in annual mean precipitation of up to 0.4cm to an increase in precipitation of up to 1m to 2080. The greatest reduction in precipitation is predicted by the GCM csiro_mk30 with the major part of the region projected to experience a decrease of between 0.05-0.4m. Whereas, the ccma_cgcm31 GCM predicts an absolute rise in precipitation of between 0.2m/yr to 1m/yr by 2080 with the majority of the region projected to experience a rise of 0.2m/yr-0.4m/yr. The remaining models most closely identify with the pattern of precipitation projected by the wettest model ccma_cgcm31. A similar pattern is observable across the Amazon basin, although the wet and dry GCMs, those which predict the largest increase and decreases of annual mean precipitation from current to 2080 are not consistent with those for the Equatorial African tropics. Projections of absolute precipitation change in the Amazon basin vary considerably across the GCMs and range between a decrease of up to -1m/yr to an increase in precipitation up to 2m/yr. The driest model is the ukmo_hadgem1 which projects that a large expanse of the Amazon basin will experience an absolute decrease in precipitation of between -0.4m/yr to -1m/yr. The ipsl_cm4 is the GCM with the wettest projection predicting absolute rise in precipitation 0.2m/yr to 2m/yr across the Amazon basin. There is also a degree of variation in model projections for South-East Asia. The model ccma_cgcm31 projects large swathes of South-East Asia to experience an increase in annual mean precipitation of between 0.2m/yr-0.4m/yr, whereas, the ipsml_cm4 predicts a drying of between -0.05m/yr and 0.4m/yr for the major part of the region rising to drying of between -0.4m/yr to -1.0m/yr in areas of Northern India.

Variation in GCM Projections across Biogeographic Zones

Zone	Temperature Change (Δ °C)	Hot Model	Cool Model	Precipitation Change (m/yr)	Dry Model	Wet Model
Palearctic	5-12	ncar_ccsm30	ccma_cgm31	0.05-0.20	■	■
Nearctic	3-8	ukmo_hadgem1	ccma_cgm31	-0.05 – 0.4	ipsl_cm4	ncar_ccsm30
Saharo-Arabian	3-5	ccma_cgm31	ukmo_hadgem1	-0.40 - 0.05	■	■
Afrotropical	1-6	mpi_echam5	ukmo_hadgem1	-0.40 – 0.40	■	ncar_ccsm30
Neotropical				-0.40 - 0.20	ipsl_cm4	■
Oriental	2-5	mpi_echam5	■	-0.40 – 2.00	csiro_mk30	ipsl_cm4
Australian	2-5	mpi_echam5	ukmo_hadgem1	-0.40 – 0.20	ukmo_hadgem1	ccma_cgcm31

Table S 6 Variation in predictions of temperature and precipitation change across the GCMs (grey highlighting shows consensus across the model set)

To investigate more fully variations in GCM patterns of future temperature and precipitation change each biogeographic region is examined in Table. Table S 6 shows the range of values predicted under the GCMs with regards to changes in temperature and precipitation for each zone and also highlights the hot/ cool and wet/dry models corresponding to each zone.

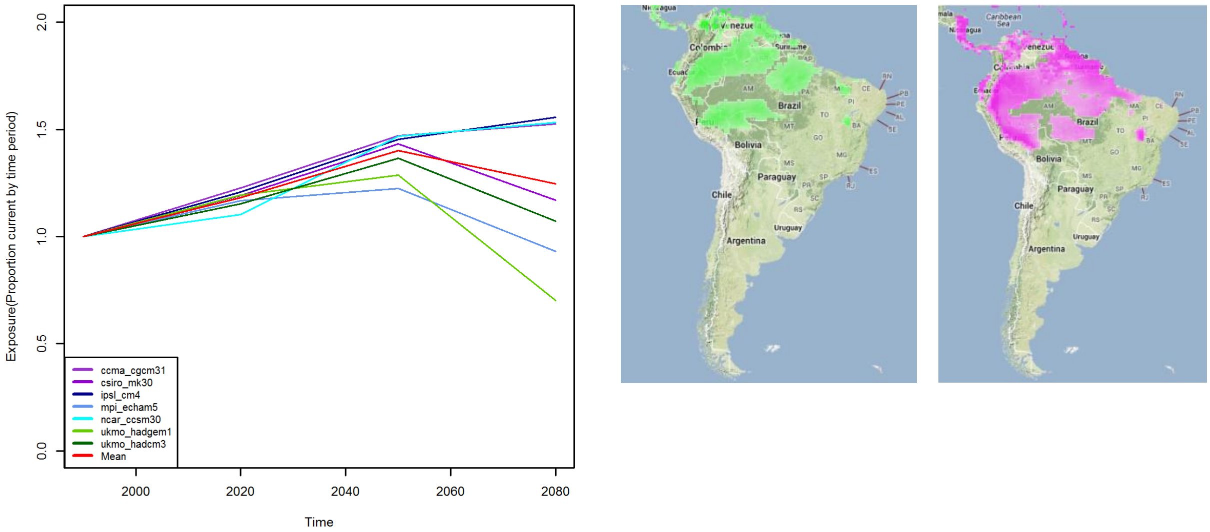
Examining the impact of climate change on species distributions by GCM

To examine how the variance in projections of climate change under the GCMs impact predictions of species future distributions under climate change time series plots were created. These plots illustrate the proportion of current distribution size projected under each of the GCMs over time. These predictions of future suitable climate space were created using a set of eight environmental variables including Annual Mean Temperature and Precipitation, Temperature and Precipitation Seasonality, Maximum Temperature of the Warmest month, Minimum Temperature of the Coldest month, Precipitation in the Wettest and Driest Quarters. These environmental variables are created using climate patterns from each of the GCMs. The species selected for closer inspection include two species whose climate niche is determined predominantly by temperature variables and two whose climate niches are driven by precipitation variables.

These figures also show the mean of the projections used to describe Exposure in Chapter Two: Calculating Future Vulnerability to Climate Change of this thesis. To minimize the effect of outlying GCMs in skewing the mean the top and bottom predictions were disregarded, and the mean was calculated across the 5 remaining GCMs. This process reduces the degree of uncertainty associated with the predictions by removing the outliers.

Temperature-driven Niche

The Common Brush-tailed Possum (*Trichosaurus vulpeca*) and the Colombian Red Howler Monkey(*Alouatta seniculus*) were selected as the environmental climate niches of both, as determined using Maxent, are dominated by temperature variables. Thus, variations within the GCMs projection of change within these environmental variations will directly impact on the prediction of suitable climate space. The Colombian Red Howler Monkey (*Alouatta seniculus*) was also chosen because its distribution falls within the Amazon basin, a region for which there is a wide range of uncertainty in mean annual temperature projections across the GCMs for 2080. The Common Brush-tailed Possum was chosen for closer analysis as a native to Australia across which the GCMs are fairly consistent in projecting mean annual temperature.



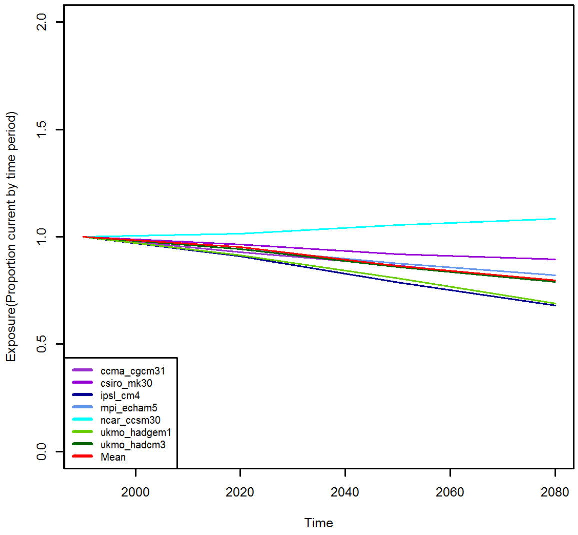
a) Exposure (Proportion of current distribution extent remaining over time) under the seven GCMs to 2080

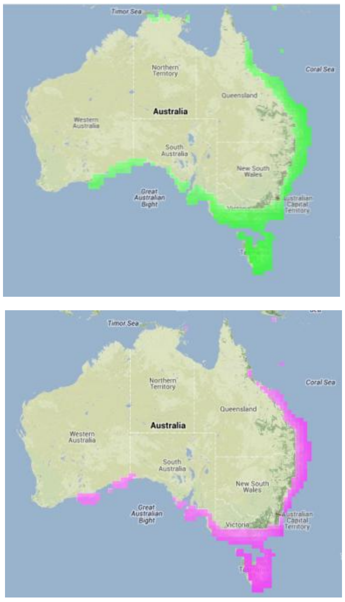
b) Current Distribution Map (Wallace Initiative)

Figure S 14 The Colombian Red Howler Monkey (Alouatta seniculus): Projections of Future Exposure (Proportion Current by time period) under the Seven GCMs and Current and Future Distribution Maps

The Colombian Red Howler Monkey, is a forest dweller native to the Amazon basin region in the North of South America (Boubli, *et al* 2008) . As has previously been discussed there is wide uncertainty between projections of mean annual temperature in the region across the GCMs. The climate niche of this monkey is predominantly determined by temperature variables (81% Temperature-driven). Patterns of precipitation as projected across the GCMs for the monkey's distribution have a standard deviation in Exposure predictions of 0.33 across the seven GCMs at 2080. Uncertainty in Exposure across the GCMs is particularly visible during the period from 2050 to 2080 (Figure S 14). Before this time period, between 2020 and 2050, each of the seven GCMs projects growth in the monkey's suitable climate space of between 11% for the most conservative estimates to 24% for the least conservative, representing a 13% range in estimates. Beyond 2050 three of the GCMs (ipsl_cm4, ncar_ccsm30 and ccma_cgcm31) continue to project growth in distribution (10% growth ipsl_cm4) and the remaining four predict a reduction in suitable climate space (66% reduction ukmo_hadcm3). Thus, at 2080 under the ipsl_cm4 GCM suitable climate space is projected to have expanded by 45%, (Exposure=1.45) whereas ukmo_hadcm3 projects a loss of 30% by 2080 (Exposure=0.70).

The uncertainty in the projections of suitable climate space between 2050-2080 stems from the underlying broad uncertainty in the GCM mean annual temperature projections which predict between a 2°C-4°C (ncar_ccsm30) up to 6°C -8°C (ukmo_hadcm3) rise in mean annual temperature to 2080. The three models which project expansion to continue 2050-2080 are those which predict the smallest degree of warming of between 2°C- 4°C. Conversely, it is the ukmo_hadcm3 model which projects the greatest degree of warming at 6°C -8°C over a large swathe of the Amazon basin. Where the top and bottom projections are clipped the mean Exposure value at 2080 is 1.24, thus predicting an increase of 24% (s.d. =0.27) in suitable climate space for the species. The projected warming in the region is reflected in the change in predicted climate space of the Howler Monkey at 2080. The monkey's distribution is predicted to expand further into the Amazon basin region as mean annual temperature rises 3-4°C, however those models projecting a greater increase in mean annual temperature 6-8°C ukmo_hadcm3) predict a reversal of the expansion seen at 2050. This might indicate that a comparatively small rise in temperature across the region suites the monkey's environmental niche beyond which it has a negative effect.





Exposure (Proportion of current by time period) under the seven GCMs to 2080

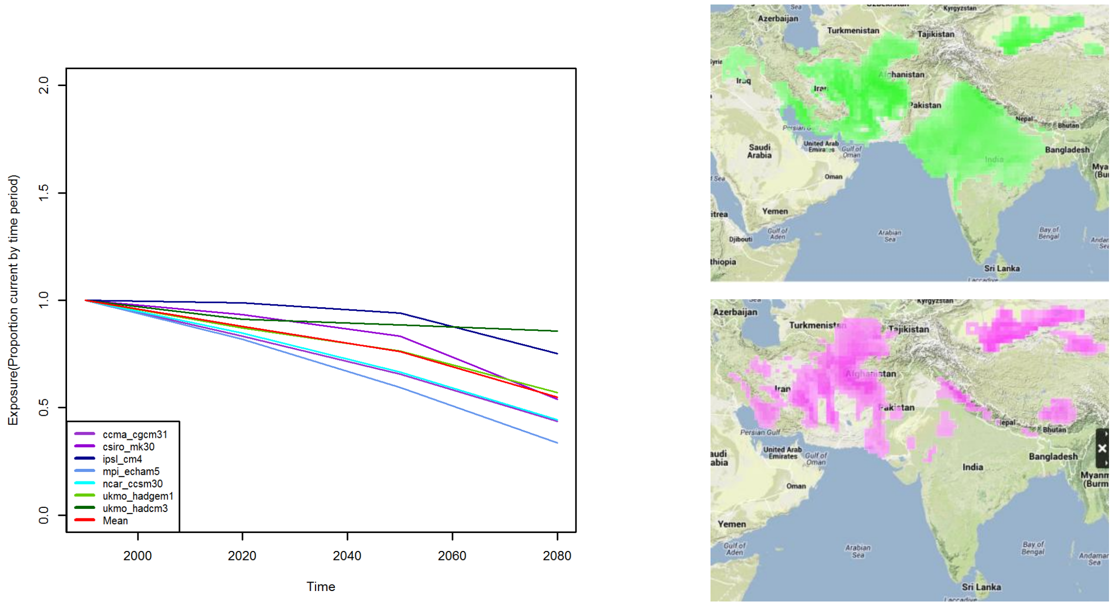
Current Distribution Map (Wallace Initiative)

Figure S 15 The Common Brush Tailed Possum (Trichosaurus vulpeca): Projections of Future Exposure (Proportion Current by time period) under the Seven GCMs and Current and Future Distribution Maps

The Common Brush-tailed Possum's climate niche, as identified in Maxent, is driven by the temperature variables, mean annual temperature and temperature seasonality, a combination of the two determining 81% of the modelled climate niche. Patterns of precipitation as projected across the GCMs for the Possum's distribution have a standard deviation in Exposure predictions of 0.13 across the seven GCMs at 2080 (Figure S 15). At 2080 mean annual temperature is projected to increase by between 3°C - 4°C across Australia under all seven GCMs. At 2020 the projections of future exposure are fairly consistent across the GCMs with a variation of 10% in potential distribution between the most (ipsl_cm4, Exposure=0.91) and least conservative (ncar_ccsm30, Exposure=1.01) estimates. These models are consistently the most and least conservative across the rest of the time period to 2080, however the variation in both broadens across the period. At 2080, this gap in estimates is equivalent to 40% of the species overall suitable climate range (ipsl_csm4, Exposure=0.67, ncar_ccsm30, Exposure=1.08). The ncar_ccsm30 is the only GCM which projects the Possum's climate space to increase by up to 8% over the period to 2080. The removal of these top and bottom estimates of suitable climate space reduces the uncertainty between the remaining GCMs to with a standard deviation of s.d. =0.07 at 2080, with a mean Exposure value of 0.79. The Possum's distribution is predicted to lose currently suitable climate space around the central Southern coast of Australia. The projected warming in Annual Mean Temperature in the region is not reflected in the change in predicted climate space of the Possum at 2080. In fact this change in distribution is relatable to changes in temperature seasonality within the region the magnitude of which is heightened around the region where the Possum is no longer predicted to occur at 2080 (Wallace Initiative 2013).

Precipitation- driven Niche

The Jungle Cat, also known as the Reed cat (*Felis chaus*) and the Eurasian Water Shrew (*Neomys fodiens*) were selected as the environmental climate niches of both species, as determined using Maxent, are both dominated by precipitation variables. The Jungle Cat was chosen because its distribution falls within the Oriental zone in a region for which high uncertainty in changes in mean annual precipitation was demonstrated across the GCMs. The Eurasian Water Shrew was selected for closer analysis as a native to the Palearctic zone across which the GCMs are fairly consistent in projecting mean annual precipitation.

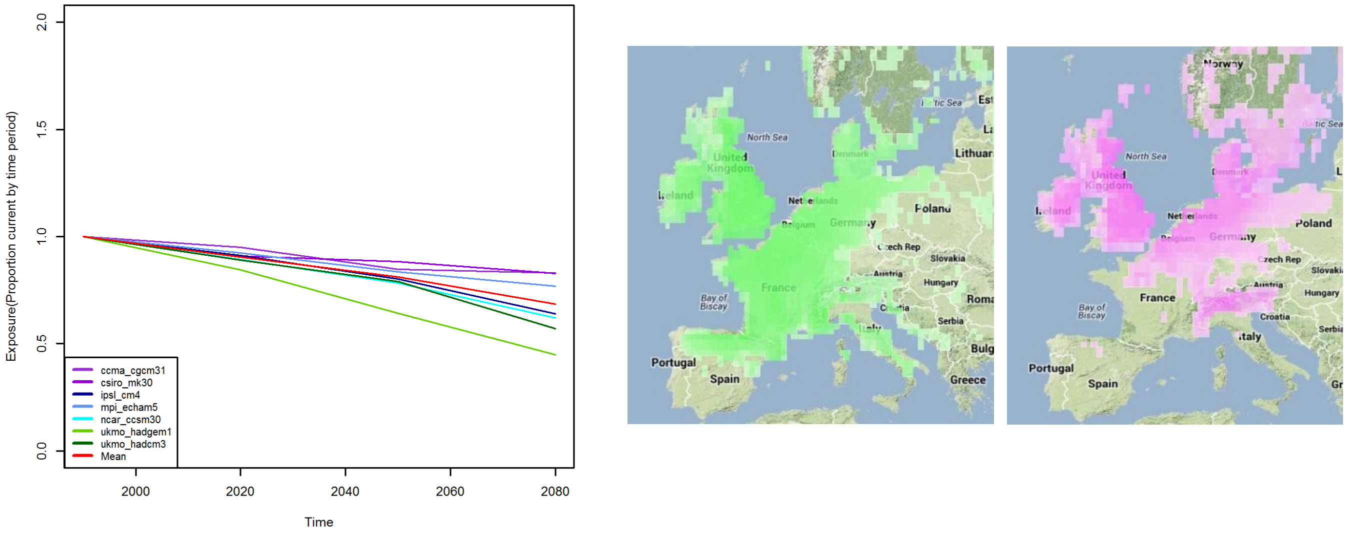


Exposure (Proportion of current by time period) and projected under the seven GCMs

Current Distribution Map (Wallace Initiative)

Figure S 16 The Jungle Cat (Felis chaus): Projections of Future Exposure (Proportion Current by time period) under the Seven GCMs and Current and Future Distribution Maps

The Jungle Cat is associated with wetlands habitat such a marsh and reed swamps and is predominantly found in India and Bangladesh although its distribution also stretches to the banks of the Nile (Duckworth *et al.* 2008). The Jungle Cat's climate niche is driven by the precipitation variables, mean annual precipitation and precipitation seasonality, a combination of the two determining 86% of the modelled climate niche. As previously alluded to there is a large degree of uncertainty across the GCMs in future mean annual precipitation across South-East Asia in which the Jungle Cat resides. The GCMs predict between an increase of 0.2m/yr-0.4m/yr (ccma_cgcm31) to a reduction of -0.05m/yr to -0.4m/yr up to -1.0m/yr in areas of Northern India (ipsl_cm4) (Figure S 16). This uncertainty in predictions of precipitation is evident in the variation across the predictions of future suitable climate space. Patterns of precipitation as projected across the GCMs for the Jungle Cat's distribution have a standard deviation in Exposure predictions of 0.17 across the seven GCMs at 2080. The models projecting the extremes of climate space at 2020 and again at 2050 are the mpi_echam 5, projecting the greatest reduction in suitable climate space with a 41% loss at 2050, and the ipsl_cm4 projecting the smallest loss of 7% at 2050. The mean value of loss in distribution at 2050 across the remaining five models is 24% s.d. =10%. At 2080 the mpi_echam model projects a further loss of distribution from 2050 of 25% (Exposure=0.33). Whereas, the ipsl_cm4 is succeeded by ukmo_hadgem1 in predicting the smallest loss at 15% by 2080 compared to 25% under the ipsl_cm4. These models both project drying within the region (-0.05m/yr to 0.40m/yr) in which the Jungle Cat is found, whilst the mpi_echam and ccma_cgcm31, the models predicting the greatest reduction in overall climate space project an increase in precipitation over the period (0.0m/yr -0.20m/yr). This would indicate that although the Jungle Cat is reliant on wetland habitats further increases in annual mean precipitation are outside of its environmental niche space, whilst it may be better able to cope with a reduction in precipitation. The majority of the models, five of the seven, project an increase in mean annual precipitation, by clipping the top and bottom predictions before calculating the mean the extreme dry and extreme wet models are removed. By removing these extremes in uncertainty the mean value is brought in line with majority of the projections resulting in a clipped mean value of Exposure=0.54 s.d.=0.17, indicating a reduction in niche space of 46%.



Exposure (Proportion of current by time period) under the seven GCMs

Current Distribution Map (Wallace Initiative)

Figure S 17 The Eurasian Water Shrew (Neomys fodiens): Projections of Future Exposure (Proportion Current by time period) under the Seven GCMs and Current and Future Distribution Maps

The Eurasian Water Shrew is a semi-aquatic species living in wetland habitat across Europe (Hutterer *et al.* 2008). The Water Shrew's climate niche is driven by the precipitation variables, mean annual precipitation, precipitation seasonality and precipitation in the driest quarter, a combination of the three determining 72.9% of the modelled climate niche. The patterns of precipitation projected across the GCMs for the Water Shrew's distribution are similar with a standard deviation in Exposure predictions of 0.13 across the seven GCMs at 2080 (Figure S 17). Across the period 2020 to 2080 it is the ukmo_hadcm3 which projects the shrew's climate niche to reduce to the largest degree to Exposure=0.44, equivalent to a loss of 66%. The model projecting the lowest degree of loss alternates between ccma_cgcm31 at 2020 and 2080 and csiro_mk31 at 2050, with an overall loss of 5-17% from 2020 to 2080. Drying of between -0.05m/yr and -0.40m/yr is projected across the Mediterranean and into Northern Europe by six of the seven GCMs. The ccma_cgcm31 is the only model to predict an increase in mean annual precipitation, restricted to parts of Northern Europe, of between 0.05m/yr -0.20m/yr by 2080. The mean loss in climate space is 32% (Exposure=0.68 s.d. =0.12). The projected drying in the region is reflected in the change in predicted climate space of the Water Shrew at 2080. The Shrew's distribution is predicted to shrink towards the Northern extent of its current range where patterns of precipitation are predicted to be more stable.

Discussion

This study sought to examine the extent to which GCMs both correspond and differ in their projections of future climate change and the impact of this related uncertainty on the prediction of future suitable climate space for species when using these projections. It also explores regional difference in the climate across the biogeographic zones identifying patterns in uncertainty.

Uncertainty associated with GCM Projections of Future Climate Change

Global Climate Patterns

In this comparison of GCM projections of both annual mean temperature and annual mean precipitation patterns regional differences in future climate change become evident. For instance differences in the degree of warming and precipitation changes become apparent between the Northern and Southern Hemisphere.

The GCM projections show that Northern latitudes and particularly the polar zone demonstrate future warming beyond that projected to be experienced in the Southern Hemisphere. A 5-12°C increase is projected across the Arctic Circle and into the tundra and this is the region for which the greatest increase in mean annual temperature is projected. This is in line with observations of land temperature since the 1980s which show that warming in the Arctic and Northern Hemisphere has been considerably faster than in the Southern Hemisphere (Armstrong 2013). The basis of this pattern of warming is relatable to inter-hemispheric differences in the impact of greenhouse gases on climate (Armstrong 2013). Warming in the Arctic Circle will increase the rate of ice melt causing the ice sheet to shrink (IPCC 2013) and negatively impacting the species which rely on the ice sheet for their survival, such as the Arctic fox (*Vulpes lagopus*) (IUCN 2009).

Assessing the GCMs with relevance to precipitation trends it is the tropical latitudes which are projected to experience the largest variation in precipitation over the coming century. The tropical zone is the region which experiences the greatest amount of annual precipitation. This is because across the tropics there is a naturally occurring belt of precipitation which moves between the Tropic of Cancer to the Tropic of Capricorn which is modulated by the Intertropical Convergence Zone (Ritter 2006). Also naturally contributing to the increased level of current precipitation across the tropics are several localised precipitation patterns which are the result of climate phenomena such as the monsoons of South Asia and Africa (IPCC 2013). It is these localised weather patterns which complicate the projection of future precipitation in the region (IPCC 2013). Precipitation decreases towards the poles due to cooler air temperatures and the associated low saturation point (Ritter 2006), resulting in less variation in annual precipitation patterns simplifying the projection of future climate change (IPCC 2013). However, this described pattern of precipitation is much simplified omitting the effect of the orientation of winds. Mountain systems and air mass dominance in influencing precipitation and which result in localised climate patterns (Ritter 2006).

Model Consistency

Exploring the projections of mean annual temperature and precipitation has allowed the identification of the GCMs which consistently project the extremes of hot or cool, dry or wet future conditions to 2080. However, agreement across the models as to which project these 'extremes' is anything but consistent and variation is evidently dependent on biogeographic region. Although the UKMO_HADGEM1 projects both the lowest global minimum and maximum mean annual temperatures and the CCMA_CGCM31 the highest mean annual temperatures these models are not consistently the coolest and warmest across the biogeographic regions. The same is true across the mean annual precipitation patterns, where MPI_ECHAM5 is the driest model projecting the smallest increases in absolute precipitation and UKMO_HADCM3 the wet model. Yet, neither of these models projects the extreme future annual precipitation values for any of the seven biogeographic zones. Uncertainty across the GCMs filters into the projections of species future distributions; this added uncertainty increases the further from current conditions projections move (Buisson *et al.* 2010). This inconsistency between GCMs, measured as contributing to up to 20% of the overall uncertainty, will determine the distribution extent predicted as pockets of suitable climate space projected under one GCM may not be projected under another (Buisson *et al.* 2010).

Projections and Regional Uncertainty

Importantly, this study identifies the regions in which the greatest uncertainty across the GCMs is apparent, but also those regions in which the GCMs projections correspond.

The greatest uncertainties in model projections of future mean annual temperature are concentrated in Equatorial Africa and the Amazon basin. Equatorial Africa and the Amazon basin are also identified as having the largest uncertainty in mean annual precipitation where they are joined by South-East Asia. These regions of high uncertainty all fall within the tropics and as such are naturally subject to greater climate variability than temperate regions (IPCC 2013; JAMSTEC 2013). This is because the climate across the tropics is governed by several smaller regional-scale climate phenomena, such as the El Niño-Southern Oscillation (ENSO), monsoons, the Indian Ocean dipole mode phenomenon and the Madden-Julian Oscillation (MJO) (JAMSTEC 2013). It is recognised that GCMs are limited in their ability to project these smaller scale climate mechanisms due to a combination of a lack of scientific understanding and computer power (IPCC 2013).

The Amazon region is affected by the El Nino-Southern Oscillation (ENSO) a weather system which develops off the western coast of South America and brings warm and very wet weather across Ecuador and Peru and drier and hotter weather to the Amazon basin. ENSO develops every 3-7 years. ENSO is projected to remain the dominant driver of interannual variability in the tropical Pacific into the 21st century (IPCC 2013). During this period ENSO-related precipitation is projected to increase due to increased moisture availability in to the coming century. However, confidence in the GCMs ability to capture the ENSO and related regional phenomena remains low, (IPCC 2013). This likely explains the uncertainty across the GCMs presented in this appendix, where some project increased warming and drying whilst others project moderate warming and increased precipitation.

The African Monsoon may be at the root of uncertainty in projections of mean annual precipitation in the rainforest region of Equatorial Africa. The African Monsoon is caused by seasonally reversing winds resulting from seasonal shifts of the Inter-tropical Convergence zone (ITCZ) and is accompanied by changes in precipitation. Uncertainty in precipitation patterns across South-East Asia is also likely to be related to the difficulty caused for GCMs associated with projecting regional climates impacted by monsoon conditions. The South Asian monsoon crosses the Indian sub-continent bringing with it 75% of the total yearly precipitation over the period June to September (Jagnnathan and Bhalme 1973). In addition to the complexities of projecting precipitation patterns driven by monsoon conditions, both the South Asian and African Monsoons are directly affected by the MJO. The MJO modulates the timing of active/break cycles which are a defining characteristic of monsoon (Matthews 2013). Monsoonal circulations are one phenomena of the climate system which have the potential to exhibit sudden or nonlinear changes due to climate change (IPCC 2007), which further complicates the projection of future climate patterns.

Across the GCMs there are two biogeographic regions in which projections of future Mean Annual Precipitation and Mean Annual Temperature are fairly consistent with no one model predicting extremes in drying or wetting, hot or cool. These regions include the temperate Palearctic and Saharo-Arabian zones. The climate in these zones is directly impacted by localised climate phenomena including the Northern Atlantic Oscillation (NAO), extra-tropical cyclones and blocking (IPCC 2007). Climate models are known to be well capable of simulating the NAO effects on both seasonal temperatures and precipitation (IPCC 2007). The phenomena of extra-tropical cyclones and blocking are short-lived phenomena (IPCC 2007) and therefore are likely to have less influence on trends of mean annual precipitation and temperature. This explains why there is less apparent uncertainty in projections of future mean annual temperature and precipitation in these regions than others.

Narrowing GCM uncertainty

This study employs several techniques in order to narrow the uncertainty in projections of future climate change and subsequently the impact of future climate change on species distributions under the business-as-usual scenario, which characterises only one of a multitude of potential future climatescapes.

There is no one best model of future climates (Beaumont *et al.* 2008). In an effort to narrow uncertainty associated with the GCM projections of future climate change an ensemble of GCMs, seven in all, are used to project future climate and from there future species distributions. In taking the average of these seven projections of future climate uncertainty associated with each is filtered out to a degree (Beaumont *et al.* 2008). However, averaging over the ensemble may introduce bias in the averaged climate projection caused by a poor model or lead to a model average representing a system unlikely to occur in nature (Beaumont *et al.* 2008). Thus, in order to avoid these pitfalls in this study the extreme model at either the end of the spectrum is removed and the average is calculated over the remaining five models.

Where uncertainty associated with GCMs can be no further reduced communication of this residual uncertainty provides awareness of the caveats associated with using GCMs to model future climate change (Beaumont *et al.* 2008). This is particularly relevant when using projections to model species future distributions.

Projections of Future Species Distributions

GCM Uncertainty and Species Projections

Uncertainty associated with the GCMs is recognised to feed into the projections of future species suitable climate space (Beaumont *et al.* 2008). The extent to which GCMs play a role in widening uncertainty in these future projections relates back to the degree of uncertainty that is inherent in their predictions of future climate for the region in which the species is located. This is evident in the trends of future suitable climate space predicted across the four species investigated in this appendix. This phenomenon is particularly apparent in the projections of the Colombian Red Howler Monkey (*Alouatta seniculus*) under each of the GCMs. The monkey is a resident of the Amazon basin region of South America. Uncertainty in this region has already been identified as broad ranging. Similarly, projections of future climate space for the Jungle Cat (*Felis chaus*) are equally divergent across the GCMs. Projections of Mean Annual Precipitation in this region are divergent across the GCMs with some models projecting an increase in precipitation whilst others predict drying in the region. This uncertainty can also be related to localised climate phenomena such as the South East Asian monsoon and the MJO.

The effect of averaging across the GCMs is evident in the projections for each of the four species examined, indicated by the red line in the diagrams of future distributions (e.g. Figure S 14). Taking the average of the projections in this way serves to smooth the uncertainty surrounding the species projections, removing a degree of the bias introduced by uncertainty in the GCM climate projections. Evidently this process is more suitable in situations where trends in projections across the GCMs are less divergent i.e. for the Possum and the Water Shrew.

Conclusion

This analysis reinforces the need for modellers of species distributions to recognise the uncertainties associated with climate projections, as advocated by (Beaumont *et al.* 2008), particularly where future distributions are used to assess the risk of future climate change. As discussed uncertainties in the GCM projections are apparent in several areas both spatial and temporal. This uncertainty relates to the way by which the Earth system is represented within the individual climate models (Buisson *et al* 2012). These underlying uncertainties are known to permeate into the projections of future species distributions, influencing the projections of future suitable climate space

(Buisson *et al* 2012). This is particularly relevant for those species resident in regions identified here as exhibiting the largest degree of uncertainty such as the Amazon.

At the individual species level these uncertainties will influence the degree to which they appear resilient to future exposure. The extent of the species' future distribution is dependent on the spatial distribution of climate space and the velocity of climate change as projected by the GCM, as well as the species dispersal capacity. This explains why distribution expansion under climate change may be projected under one GCM but contraction under another. By creating an ensemble of distributions projected under a suite of seven GCMs and taking a consensus approach as in this thesis the degree of uncertainty is lessened although not removed.

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List of Acronyms

ANOVA	Analysis of Variance
ANCOVA	Analysis of Covariance
AR4	IPCC Fourth Assessment Report
AR5	IPCC Fifth Assessment Report
Bioclim	Bioclimatic variables (Hijmans *et al.* 2005)
BP	Before present
CO_2	Carbon Dioxide
CO_2e	Carbon Dioxide Equivalent
GCM	Global circulation model
GHG	Greenhouse Gas
GLM	General linear model
Gtc/yr	Gigaton carbon per year
$GtCo_2$	Gigaton carbon dioxide
GBIF	Global Biodiversity Information Facility
GLM	General Linear Model
IPCC	Intergovernmental Panel on Climate Change
km^2	Kilometres squared
km/yr	Velocity (Kilometres/ year)
LHTd1084	Life History Traits Database 1084 species
LHTd213	Life History Traits Database 213 species
m	Metre
m/yr	Metres per year
Ma	Mega-annum (Million years ago)
PCAi	Initial Principal Components Analysis
PCAf	Final Principal Components Analysis
S.D.	Standard Deviation
SRES A1B	IPCC Emissions scenario A1B

Supplementary Material S1: Traits Cluster Diagram

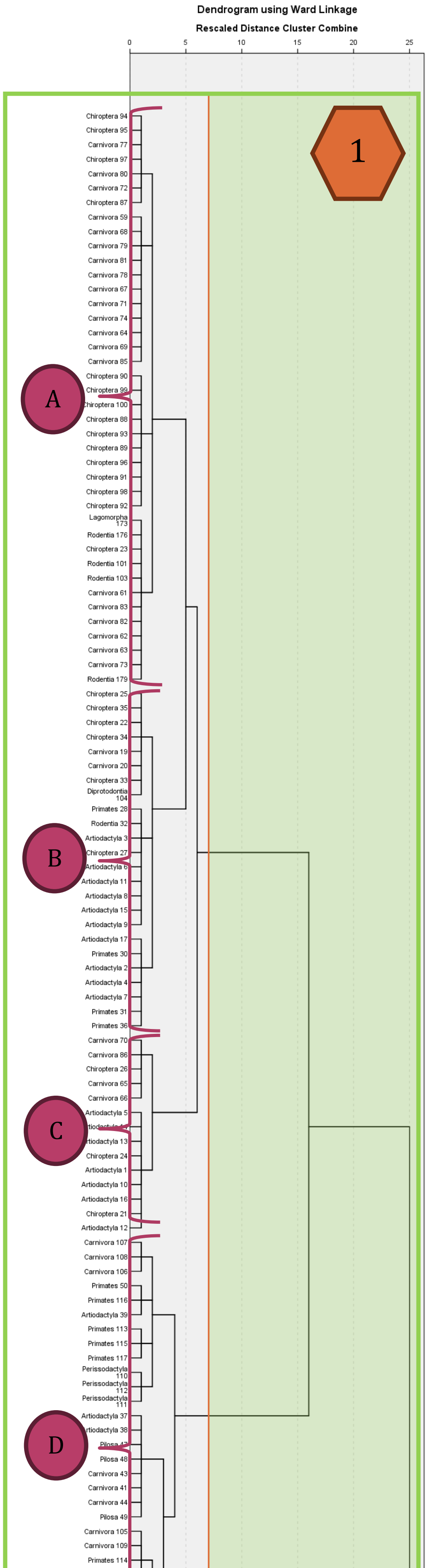

Figure 1: A Cladogram created using the traits identified as determining Sensitivity (Excluding Endemicity).

Two dominant branches were identified and eight clusters (branches 1-2, clusters a-g).

Supplementary Material S2: Taxonomy

The taxonomy used for the placental mammals, the Eutheria, is adapted from Beck et al (2006). However, because marine species were excluded from the analysis the Order Cetartiodactyla is again split into Cetacea (the Whales) and Artiodactyla (even-toed ungulates) to bring clarity to what is being modelled and investigated. The taxonomy for the Marsupials (Infraclass Marsupalia) adopts the taxonomy developed by Wilson and Reeder (2005).

Infraclass	**Superorders**	**Orders**	**Order Common Names**	**Included in LHTd213 Analysis**
Eutheria	Afrotheria	Hyracoidea	Hyraxes	Yes
		Proboscidea	Elephant	No
		Sirenia	Seacows	No
		Afrosoricida	African ‘insectivores’ (tenrecs and golden moles)	No
		Macroscelidea	Elephant shrews	Yes
		Tubilidentata	Aardvark	No
	Xenartha	Cingulata	Armadillos	**Yes**
		Pilosa	Anteaters and sloths	Yes
	Euarchontonglires	Lagomorpha	Lagomorphs	Yes
		Rodentia	Rodents	Yes
		Dermoptera	Flying Lemurs	No
		Primates	Primates	Yes
		Scandentia	Tree shrews	Yes
	Laurasiatheria	Eulipotyphla	True ‘insectivores’ (hedgehogs, shrews, true moles and *Solenodon*)	Yes
		Carnivora	Carnivorans	Yes
		Artiodactyla*	Even-toed ungulates	Yes
		Perrisodactyla	Odd-toed ‘ungulates’	Yes
		Pholidota	Pangolins	No
		Cetacea*	Whales	No
		Chiroptera	Bats	Yes
Marsupalia	Australidelphia	Diprotodontia	Australian marsupials (kangaroos, wallabies etc.)	No
		Peramelemorphia	Bandicoots and bilbies	No
		Microbiotheria	Monito del monte	Yes
		Noctorycetemorphia	Marsupial moles	No
		Dasyuromorphia	Marsupial carnivores	No
	Ameridelphia	Paucituberculata	Shrew opossums	No
		Didelmorphia	American opossums	Yes
Prototheria		Montremata	Echidna and Platypus	No

Table 1 Taxonomy follows that outlined for the placental mammals in Beck et al (2006) *except Cetartiodactyla is split into Cetacea and Artiodactyla because marine species are excluded from this analysis.

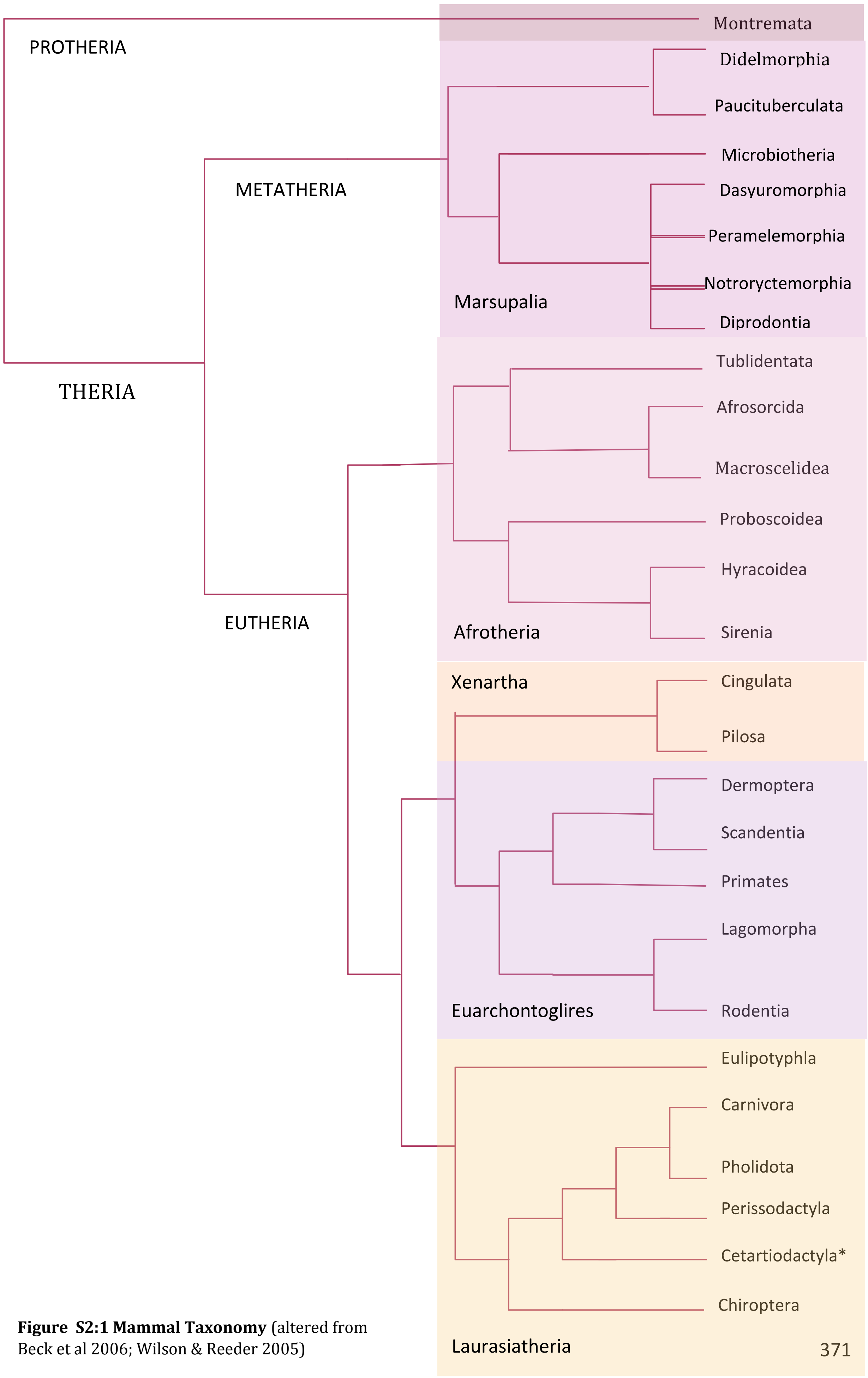

Figure S2:1 Mammal Taxonomy (altered from Beck et al 2006; Wilson & Reeder 2005)