The ecological impacts of human-modified landscapes on vertebrate communities in Southeast Asia

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Abstract

Hydropower development and oil palm agriculture are two of the most important drivers of habitat fragmentation and degradation of tropical forests globally. This thesis assesses how these human modified landscapes are impacting vertebrate communities in Southeast Asia. Using a dataset from an archipelago of island forest fragments embedded within a hydroelectric reservoir in Thailand spanning three decades, my second chapter documents the near-complete collapse of a small mammal community driven by the generalist Malayan field rat, which outcompeted all other native species and accelerated their local extinction rates. In chapter three, I combined data from chapter one with two other hydropower reservoirs in Southeast Asia – spanning a gradient of human disturbance – to assess the role habitat degradation plays in the species-area relationship (SAR). The collapse of SARs in degraded landscapes emphasized the impacts of habitat degradation along with hyperabundant generalists on small mammal species richness, improving conventional SAR predictions. In chapter four, using camera trap surveys across the same sites as chapter two, I reveal that adding a proxy for habitat degradation to the equilibrium theory of island biogeography (ETIB) improves the power of this well establish ecological framework to predict vertebrate responses to habitat fragmentation. In chapter five, I used a regional camera trapping dataset to quantify the rise of hyperabundant native generalists – wild pigs and macaques – in proximity to oil palm dominated landscapes throughout Southeast Asia. While most species are suffering in these human altered forests, a few species have benefited greatly; understanding the traits that may predispose species to benefit from land-use change and their consequences on the ecosystem will be paramount in decades ahead. My thesis contributes towards our understanding of how increasing proliferation of hydroelectric dams and oil palm will drive changes in ecological communities, species distributions and their interactions with humans.

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Contents

List of tables

List of supplementary tables

List of figures

List of supplementary figures

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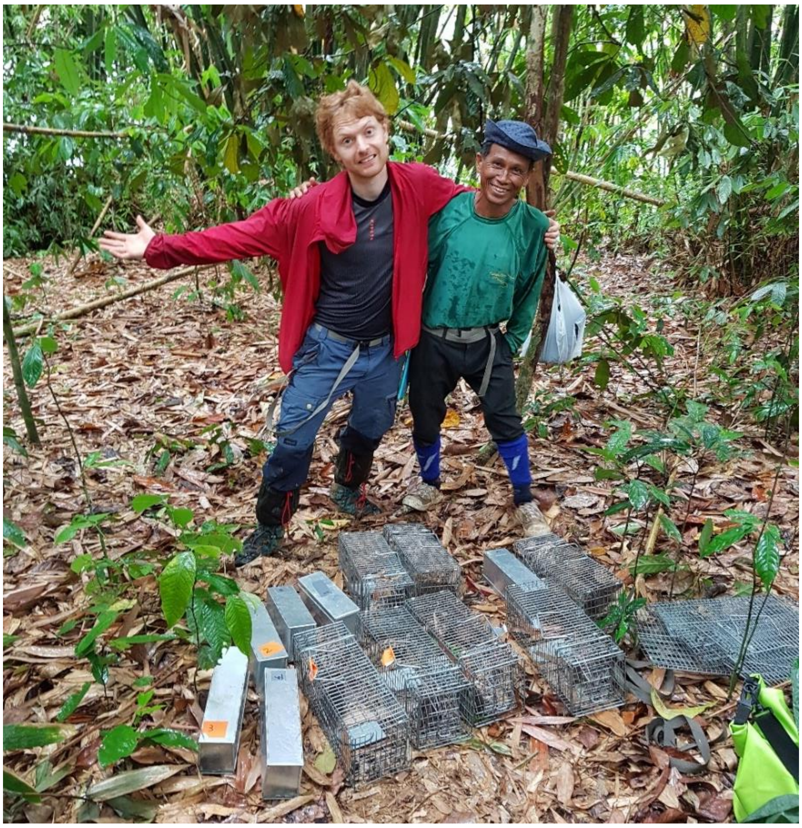

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Chapter 1 Introduction

Anthropogenically induced habitat alteration

Up until recent years the Holocene Epoch, which began around 11,650 years ago, defined the geological time scale in which we lived, with a warming Earth and subsequent glacial retreat (Wanner et al., 2011). However, at present a debate as to a newly defined geological Epoch has begun, termed the "Anthropocene", which is defined by the unprecedented impact human activity has had on the Earth (Brown et al., 2013; Piperno et al., 2015). Currently it is estimated that 95% of the Earth's surface shows some form of anthropogenic modification (Ellis, 2021; Foley et al., 2005; Kennedy et al., 2020), leaving only 40% of forests globally with high ecosystem integrity (Grantham et al., 2021) and >70% of the world's remaining forests within 1 km of an edge (Haddad et al., 2015).

This unprecedented level of human mediated landscape alteration occurring on a global scale is the primary driving force of what many scientists believe is the starting point of the Earth's sixth mass extinction, based on the rates of species loss which are now 100 times higher than expected levels within the background fossil record (Barnosky et al., 2011; Pimm et al., 2014). Habitat alteration is contributing to the defaunation of large landscapes (Dirzo et al., 2014), causing decreases in reptile populations (Doherty et al., 2020), intensifying the decline in bird populations (Bregman et al., 2014) and driving primates to extinction globally (Torres-Romero et al., 2023).

Human landscape alterations occur for a variety of purposes. Urbanization has given rise to extensive road networks, infrastructure, and demands for housing, transportation, and utilities leading to extensive modifications in the physical characteristics of the landscape (Concepción et al., 2015; Liu, Coomes, et al., 2019; Simkin et al., 2022). Industrialization, a key driver of economic growth, requires large-scale energy production to fuel factories and manufacturing processes (Ahmed et al., 2022). Resource extraction for valuable materials, including precious metals like diamonds, gold, and lithium, as well as hardwoods, increases additional landscape transformations (Bebbington et al., 2018). By far the biggest driver of this transformation is agricultural expansion, considered a global threat to biodiversity with an extensive body of literature demonstrating negative effects on mammal (Kehoe et al., 2015), bird (Tscharntke & Batáry, 2023), reptile (Ribeiro et al., 2009) and plant diversity (Laurance et al., 2014). The livestock industry, further contributes to landscape alterations through the creation of pasture lands and large-scale feed crops (Coimbra et al., 2020). Other large-scale agriculture, (illustrated in chapter 5 of this thesis by oil palm plantations), has become a leading force transforming tropical ecosystems and contributing to deforestation and the disruption of local communities (Descals et al., 2021; Vijay et al., 2016). All of these activities are driven by the needs of >8 billion people, whose water requirements are expected to increase up to 20-30% by 2050 (Burek et al., 2016); while energy requirements are expected to increase up to 50% by 2050, particularly in heavily industrialized developing countries (herein illustrated by hydroelectric dams) (IEA, 2021).

Hydropower reservoirs

Although considered a “green” renewable energy source, the construction of hydroelectric reservoirs has a serious negative effect on the natural habitats and biodiversity in high conservation value regions (Gibson et al., 2017). Over 8,600 of these hydroelectric reservoirs exist globally (ICold, 2019), with an additional 3,700 dams planned, mainly in emerging developing countries (Zarfl et al., 2015). These planned dams are the result of increasing demands for energy and water (Burek et al., 2016), aggravated by commitments to increasing renewable energy production (Wasti et al., 2022). For example, Brazil is rapidly expanding hydropower capacity with an additional 277 dams planned for construction (Castello et al., 2013; Lees et al., 2016) in areas with steep topography and high rainfall which are ideal for electricity generation (Finer & Jenkins, 2012).

Globally, hydropower generates over 1,292 GW or 4,200 terawatt hours (TWh), which accounts for two thirds of renewable energy production. At the regional scale, 50% of all energy production in South and Central America now comes from hydropower (IEA, 2021), while in South and Southeast Asia, 14.5% of all energy production is now contributed by hydropower. South and Southeast Asian hydropower has a capacity of 117 GW, which is expected to grow further to meet the demands of the region (IEA, 2021).

Large-scale oil palm plantations

Large-scale conversion of natural forest ecosystems to agricultural plantations has also caused enormous alterations in tropical forest ecosystems. Agricultural expansion occurred rapidly during the 1980s and 1990s, in which 55% of new agricultural land resulted in the clearance of intact forests, while a further 28% involved the clearance of disturbed forests (Gibbs et al., 2010). Various forms of large-scale agriculture exist such as soybean, wheat, corn and cotton, however oil palm plantations now dominate extensive landscapes on a global scale, covering >27 Mha (Cheng et al., 2018; Descals et al., 2021). Southeast Asia in particular is a heavy oil palm producer accounting for almost 90% of global production (Danylo et al., 2021). The current expansion of oil palm plantations is driven by the energy sector to produce biofuels; by the global food system, to produce food and animal feed;

and by the industrial demand for oleochemicals, used in the composition of household and cosmetic products (Bausano et al., 2023; Fitzherbert et al., 2008; Mba et al., 2015). The high demand for oil palm across a variety of sectors is a major concern for the future. It has been estimated that 234 Mha are suitable for further conversion into oil palm plantations globally (Pirker et al., 2016), which is likely to happen at the expense of natural ecosystems and native biodiversity.

Consequences for ecosystems and biotic communities

These two processes of human landscape alteration have major implications for ecosystems and biotic communities. For example, the artificial lakes created during the construction of hydropower dams flood extensive areas of habitat often occurring within highly diverse lowland forest ecosystems - and sometimes with the presence of indigenous communities (Lees et al., 2016). The hydroelectric dams represented in this doctoral thesis have created artificial lakes ranging in size from 165km^2 up to 2,600 km^2, which is typical of this form of infrastructure. The resulting landscape is a fragmented mosaic of islands of varying size, the remnants of forested hill tops, surrounded by a matrix of water.

The subsequent habitat fragmentation causes an increase in the number of habitat patches through the removal of habitat, generating inhospitable stretches of landscape (J. T. Curtis, 1956; N. W. Moore, 1962). This fragmentation subsequently triggers edge effects that gradually degrade the remaining plant communities over the following decades (Murcia, 1995; Pfeifer et al., 2017) while also creating a barrier to the movement and dispersal of terrestrial animals. The interplay between modified plant communities and isolation can impact animal communities in various ways, influencing species composition, population dynamics, potential dominance by a few or single species, loss of genetic variability, and accelerating local extinction rates, which is contingent upon the life history traits and taxonomic group of the organisms involved (Bender et al., 1998; Fahrig, 2003; Gibson et al., 2017; Lees et al., 2016).

Similarly, the cultivation of oil palm plantations often leads to deforestation, habitat loss, fragmentation and degradation of the surrounding landscape, with research showing that 56% of Indonesian and 59% of Malaysian oil palm expansion came at the expense of forest between 1990 and 2005 (Asner et al., 2009; Koh & Wilcove, 2008; Rudel et al., 2009). What results following conversion of a forested landscape into oil palm is a monoculture of the oil palm species *Elaeis guineensis*, clearing expansive areas of native flora to produce a homogenized landscape, devoid of natural food sources, with reduced niche availability due to an extremely simplified forest structure, and altered microclimatic conditions (Sayer et al., 2012; Vijay et al., 2016). This dramatic alteration of the landscape has major implications for the resident animal communities, supporting fewer species particularly those of conservation importance (Fitzherbert et al., 2008).

In both scenarios of habitat alteration, forest specialists are the most vulnerable species to these processes with over 4000 species impacted (Filgueiras et al., 2021; Maxwell et al., 2016; Tabarelli et al., 2012), as habitat specialists often struggle to adapt due to their specific resource requirements and narrow dietary breadths which are subsequently negatively affected (Betts et al., 2017; Henle et al., 2004). In contrast, some species have the potential to exploit these newly formed anthropogenic niches depending on their life history traits, with generalist species that possess a high tolerance to human presence, high dispersal capability and an opportunistic foraging strategy (Clavel et al., 2011; Devictor et al., 2008; Gibson et al., 2011) more likely to thrive.

Thesis aims and structure

This PhD thesis represents an effort to understand which species can adapt to Earth's rapidly changing landscape conditions, either as a response to the effects of either habitat fragmentation or to large-scale oil palm plantations. The thesis is primarily based on two datasets; the first dataset (Chapters 2-4) spans two countries and three landscapes, consisting of an array of island fragments formed following inundation for the creation of hydroelectric dams, testing key components of the Equilibrium Theory of Island Biogeography (ETIB) (MacArthur & Wilson, 1963, 1967) and the species-area relationship (SAR) (Lomolino, 2000a). The second dataset (Chapter 5) spans Southeast Asia, Borneo and Sumatra and consists of >60 landscapes, exploring the extent to which a select group of habitat generalists are capable of thriving within both oil palm dominated and degraded landscapes.

Part 1: Effects of habitat fragmentation induced by hydropower dams on terrestrial vertebrate communities

To address my research questions relating to the impacts of fragmentation, first I had to choose the appropriate study sites. To ensure a successful project, several requirements needed to be considered: 1) a fragmented landscape with range of different sized islands, 2) similar durations since the initial fragmentation event, 3) a study site with a long-term dataset following the trajectory of an animal community, and 4) a degradation gradient between fragmented landscapes.

With these criteria three hydropower dam landscapes were selected. Each landscape was formerly an intact rainforest ecosystem before being designated as a site to build a hydropower dam. Each landscape was subsequently flooded at relatively similar time periods, inundating large areas of the forest, and leaving a fragmented insular island landscape with a range of island sizes surrounded by an inhospitable water matrix (Figure 1.1). All sites also existed across a disturbance gradient and one site also had two previously published datasets following the trajectory of a small mammal community through time (Gibson et al., 2013; Lynam & Billick, 1999). Each of these fragmented landscapes subsequently acted as a man-made laboratory setting allowing me opportunities to understand the impacts of habitat fragmentation on the residing animal communities.

Figure 1.1. Landscape views of island forest fragments embedded within hydroelectric reservoirs.

Chapter 2

Chapter 2 was designed to take advantage of an existing dataset at Chiew Larn reservoir in Thailand, at which previous work studying the small mammal community had been conducted in 1992-94 (Lynam & Billick, 1999) and 2012-13 (Gibson et al., 2013). Long term datasets following the trajectory of small mammal communities after an initial isolation event are rare within the literature but are important to understand ‘extinction debts’, which occurs when species experience a post-isolation relaxation period over the coming years and decades (Diamond, 1972; Ewers & Didham, 2005; Tilman et al., 1994). This provided the opportunity to understand the rate at which small mammal assemblages decline over a 33-year time period and determine the modulating variables that may have contributed to this decline.

To do this I matched the sampling design employed in both studies previously conducted at Chiew Larn, sampling the same set of fragmented islands and using the same techniques to survey small mammals (Figure 1.2). This involved similar trapping equipment, protocols and using the same level of effort to allow for comparable data on the trajectory of the small mammal community (Figure 1.3). I then expanded on work performed by (Lynam & Billick, 1999) and (Gibson et al., 2013) by incorporating the impacts of a generalist rodent, the Malayan field rat (*Rattus tiomanicus*), as a modulating variable for the decline of other native small mammals in my models to test if this could better explain community trends compared to the traditional ETIB modelling framework.

Figure 1.2. Examples of small mammal survey equipment; tomahawk trap, sherman trap, measuring and tagging equipment including volunteers and staff (left to right).

Figure 1.3. Rodent species caught (A) *Rattus / Tiomanicus*, (B) *M. berdmorei*, (C) *L. sabanus*, (D) *C. gliroides*, (E) *M. surifer*, (F) *N. fulvescens.*

Chapter 3

Chapter 3 was designed to utilize the gradient of disturbance that exists between the three fragmented insular landscapes, to understand how small mammal communities respond to habitat degradation. The chapter attempted to test if including modulating variables into predictive models such as habitat degradation along with the dominance of an invasive rodent could better explain species trends compared to the traditional ETIB framework. Increasing numbers of studies are now testing the limitations of the ETIB framework in explaining community structures by incorporating additional explanatory variables over standard models that include only island area and isolation distance (Lomolino, 2000b).

To do this, I surveyed the small mammal communities at all three landscapes using the same protocols employed in Chapter 2 for a similar range of island sizes (Figure 1.4). I then chose to use the Normalized Difference Vegetation Index (NDVI) as a proxy for habitat degradation which is a widely used metric providing information on canopy openness and health of the forest (Pettorelli et al., 2005) and has been used in a multitude of studies to understand the impacts of landscape degradation on animal communities (Elbahi et al., 2023; Holm, 2003; Thiam, 2003; Vogelmann et al., 2017). These data allowed me build models to understand the degree to which the ETIB framework can explain observed species trends or if additional modulating variables were more important. This expanded on Chapter 2 by incorporating a multi-landscape scale dataset to address the impacts of habitat degradation and invasive species dominance in more detail.

Figure 1.4. Rodent species caught (A) *Rattus / Tiomanicus*, (B) *T. glis*, (C) *S. muelleri*, (D) *C. gliroides*, (E) *M. surifer*, (F) *N. fulvescens*, (G) *E. gymnura*.

Chapter 4

Chapter 4 was designed to take the concepts employed within Chapter 3 but expand this to the terrestrial vertebrate community to understand how the richness of the vertebrate community responded to increasing levels of degradation. The terrestrial vertebrate community is comprised of a more diverse array of animals than just the small mammal community, with a greater range of traits and niche requirements (Figures 1.5 & 1.6). I aimed to test if the importance of habitat degradation as a predictor variable would increase as the overall landscape degradation increased. I also wanted to assess the limitations of the ETIB framework in explaining the observed trends, as there is a growing body of literature showing the importance of including additional modulating variables such as habitat degradation in models to explain species community trends (Koh & Ghazoul, 2010; Matthews et al., 2016; Triantis et al., 2012).

To do this, I surveyed islands of varying size and mainland sites at all three insular fragmented landscapes using camera traps. This allowed me to generate a dataset containing the richness of terrestrial vertebrates on both islands and within the mainland. I then collected NDVI data acting as a proxy for habitat degradation along with other traditional variables such as island area and isolation distance. Combining this data at a multi-landscape scale, I was able to assess if including habitat degradation along with the traditional ETIB variables provided models that better explain community richness. I then performed modelling at the individual landscape level with both ETIB variables and habitat degradation to determine if the importance of the habitat degradation variable increased as habitat disturbance increased between landscapes.

Figure 1.5. Species located at contiguous forest (CF) sites:(A) *Catopuma temminckii*, (B) *Rusa unicolor*, (C) *Elephas maximus*, (D) *Bos gaurus*, (E) *Neofelis nebulosa*, (F) *Helarctos malayanus*.

Figure 1.6. Species located on islands: (A) *Catopuma temminckii*, (B) *Sus scrofa*, (C) *Manis javanica*, (D) *Bos gaurus*, (E) *Hystrix brachyura*, (F) *Macaca nemestrina*.

Part 2: Effects of oil palm subsidies and landscape degradation on the abundance of generalist species

Chapter 5

Chapter 5 focused on another major form of habitat alteration, the conversion of forests to oil palm plantations and how animal communities respond to the changes. The chapter was developed in response to the growing number of cases documenting hyperabundant species globally (J. H. Moore et al., 2022; Taylor et al., 2016; Valente et al., 2020) and how oil palm subsidies have the potential to increase the abundance and densities of generalist species (Ickes, 2001; Love et al., 2017; Luskin et al., 2014) compared with the abundance of other animal species. This is a trend that is occurring globally in which generalist species are thriving while specialist species are declining (Filgueiras et al., 2021).

To address this research topic, I chose to focus on the Southeast Asian region which is dominated by oil palm plantations. I then chose a select group of generalist species for their potential to be positively impacted by oil palm subsidies based on their advantageous traits (Barrios-Garcia & Ballari, 2012; Bieber & Ruf, 2005). Focusing within the natural distribution of the target generalist species (Figure 1.7), I then collected three datasets, two at the regional scale (using a literature search) and one at the individual landscape scale (performing new camera trapping). The first regional scale dataset examined the detection histories of 89 terrestrial vertebrates >1 kg extracted from 43 camera trapping studies spanning 58 landscapes, looking at relative abundance. A second regional scale dataset focused on species densities extracted from 61 publications, spanning 41 landscapes. A third individual landscape dataset used newly collected camera trap data from 10 landscapes, providing more detailed abundance data of vertebrate species. These three datasets were used to test if the observed trends were consistent across different metrics, increasing the support for any conclusions made. I then performed modelling to understand how generalists responded to both oil palm dominated landscapes and degraded landscapes compared to other vertebrate species. This chapter addressed an important research gap in understanding how oil palm is impacting vertebrate communities leading to cascading effects within the environment.

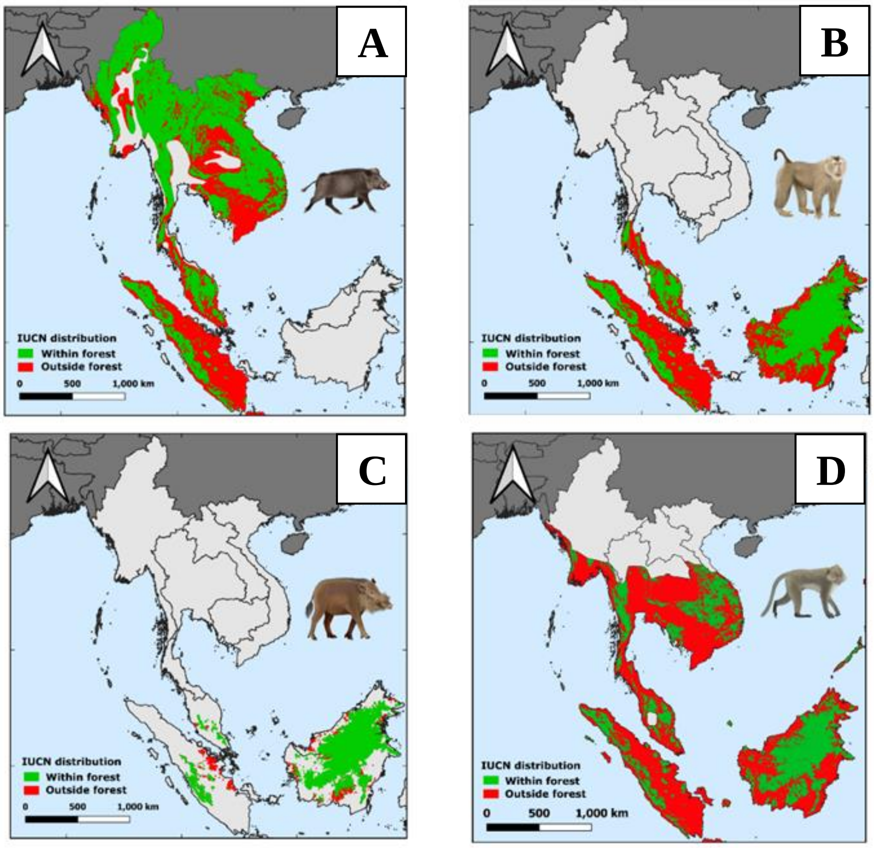


Figure 1.7. IUCN distribution maps within Southeast Asia, of wild boars (A), pig-tailed macaques (B), bearded pigs (C), and long-tailed macaques (D). For A-D, the species range is shown in areas within forests (green) and outside forest (red).

Chapter 6

Finally in Chapter 6 I conclude with my primary findings, ecological implications and lessons learnt. I also provide all supplementary materials separated by chapter.

Chapter 2 : Invasive rat drives complete collapse of native small mammal communities in insular forest fragments

Abstract

As tropical forests are becoming increasingly fragmented, understanding the magnitude and timeframe of biodiversity declines is vital towards 21st century sustainability goals. Over three decades, I monitored post-isolation changes in small mammal species richness and abundance within a forest landscape fragmented by the construction of a dam in Thailand. I observed a near-complete collapse of species richness within 33 years, with no evidence of a re-colonization effect across repeatedly sampled islands. My results further revealed a decline in species richness as island size decreased and isolation time increased, accelerated by the increasing dominance of the ubiquitous Malayan field rat, *Rattus tiomanicus*. This species was already hyper-abundant on smaller islands in the initial surveys (1992-1994, 66% of individuals) but became monodominant on all islands regardless of island size by the most recent survey (2020, 97%). My results suggest that insular forest fragments are highly susceptible to rapid species loss, particularly due to the competitive nature of *Rattus* accelerating the rate at which extinction debts are paid. To mitigate these impacts, reducing the extent of habitat degradation, as triggered by fragmentation and exacerbated by isolation time, can help to sustain native biodiversity while averting *Rattus* hyper-abundance.

Introduction

Tropical forest loss and fragmentation have increased rapidly on a global scale, induced by logging and conversion of landscapes for human infrastructure (P. G. Curtis et al., 2018; Grantham et al., 2021). Only 41% of all remaining forests are currently classified as high-integrity landscapes (continuous blocks of unmodified naturally regenerated forest), with only 17 mega-fragments (areas >100,000 km^2) remaining pantropically (Taubert et al., 2018) . Forest landscapes dominated by small fragments are also experiencing accelerated deforestation rates (Haddad et al., 2015; M. C. Hansen et al., 2020). These fragmented landscapes subsequently experience changes in the vegetation structure, creating potentially unfavourable habitat conditions induced by edge effects (Liu, Slik, et al., 2019).

Biological assemblages isolated in forest fragments typically experience a novel hyper-disturbance regime, resulting in drastic shifts in species diversity and community composition through species extinction and turnover (Fahrig, 2003; Haddad et al., 2015). Responses to fragmentation further depend on species-specific life history traits with long-term persistence potentially favouring species with fast life-histories, generalist diets, and an ability to traverse matrix habitats that separate fragments (Filgueiras et al., 2021). As most species residing within biodiverse tropical forests are forest specialists, they often suffer disproportionate declines or even extinction when exposed to human modified landscapes; the declines of these species are mediated by competitively inferior functional traits including small body size, reduced aggression, limited mobility, dietary specialization and habitat specialization (Betts et al., 2017; Fritz et al., 2009; Henle et al., 2004; Newbold et al., 2014).

Such changes in species assemblages generally exhibit an ‘extinction debt' in which species experience a post-isolation relaxation period over the coming years and decades (Ewers & Didham, 2005; Tilman et al., 1994). It is therefore important to understand the time frame and extent to which species are lost following fragmentation. The equilibrium model of island biogeography theory (ETIB) was first developed to explain the variation in species richness in archipelagic landscapes using two predictors of species richness: island area (representing carrying capacity) and distance to mainland (representing immigration rates from source populations) (MacArthur & Wilson, 1963; Preston, 1962). ETIB states that more isolated smaller islands have higher extinction rates with lower immigration rates resulting in fewer species than less isolated larger islands. ETIB has been empirically tested by multiple studies (Kalmar & Currie, 2006), however although the ETIB has been integral central paradigm in ecology, conservation biology and island biogeography, modern ecology is dealing with unprecedented changes in landscape structure through large-scale fragmentation exposing potential limitations of ETIB in explaining species richness patterns (Lomolino, 2000b).

Local species interactions are rarely considered as modulators of both ETIB curves and ‘extinction debts’, such as how hyper-dominant rat species might interact with other native species and accelerate the rate at which their ‘extinction debts’ are paid. The genus *Rattus* has invaded at least 80% of the world’s island groups (Harris, 2009), threatening native faunal communities (Harper & Bunbury, 2015; Harris, 2009; Towns et al., 2006). Yet the extent to which and timeframe of extirpations on islands may be affected by the hyper-abundance of invasive species remains poorly understood. This is challenging due to the general lack of long-term datasets following the trajectory of an animal community over multiple decades. This is compounded by the lack of research involving the impacts of hyper-dominant native species within insular fragments. Here I document the first complete chronosequence of an extinction debt in a human-made archipelago.

The overall aim of the study is to understand how habitat loss and insular forest fragmentation drives the persistence of small mammal communities over time. To address this, I repeated previous work conducted in 1992-94 and 2012-13 (Gibson et al., 2013; Lynam & Billick, 1999) focused on the same small mammal communities isolated on island fragments in Chiew Larn reservoir, a 165 km^2 hydroelectric impoundment in Thailand (Figure 2.1). In 2020, I conducted a third survey, completing a detailed timeline of the decline in species richness and abundance in response to fragmentation spanning 33 years. I used these data to quantify the rate at which native small mammal species richness and abundance changed over time, the rate at which hyper-abundance of a generalist rodent increased over time, and to identify the primary drivers impacting the trajectory of small mammal richness and abundance using path analysis. Finally, I discuss the implications of the results in the context of the equilibrium theory of island biogeography (ETIB) and the rate at which ‘extinction debts’ are paid (Ewers & Didham, 2005; Tilman et al., 1994).

Methods

Study area

This study was conducted at Chiew Larn reservoir in Surat Thani province, Thailand (9°07'35.9"N, 98°37'24.2"E) (Figure 2.1). The landscape consists of lowland monsoon evergreen forest with a mosaic of successional stages, exposed to a mean annual rainfall of 2,365 mm and mean annual temperatures of 26.8°C. The impoundment reservoir flooded 165 km^2 of forest following construction of Rajjaprabha Dam, completed in 1987. In the process, more than 100 islands were formed within the reservoir, ranging in size from <1 to >100 ha (mean size ≈ 8 ha). The forest surrounding the reservoir is divided between two major protected areas, including Khlong Saeng Wildlife Sanctuary, originally established in 1974 and covering 1,155 km^2. This forest served as a useful continuous forest control site.

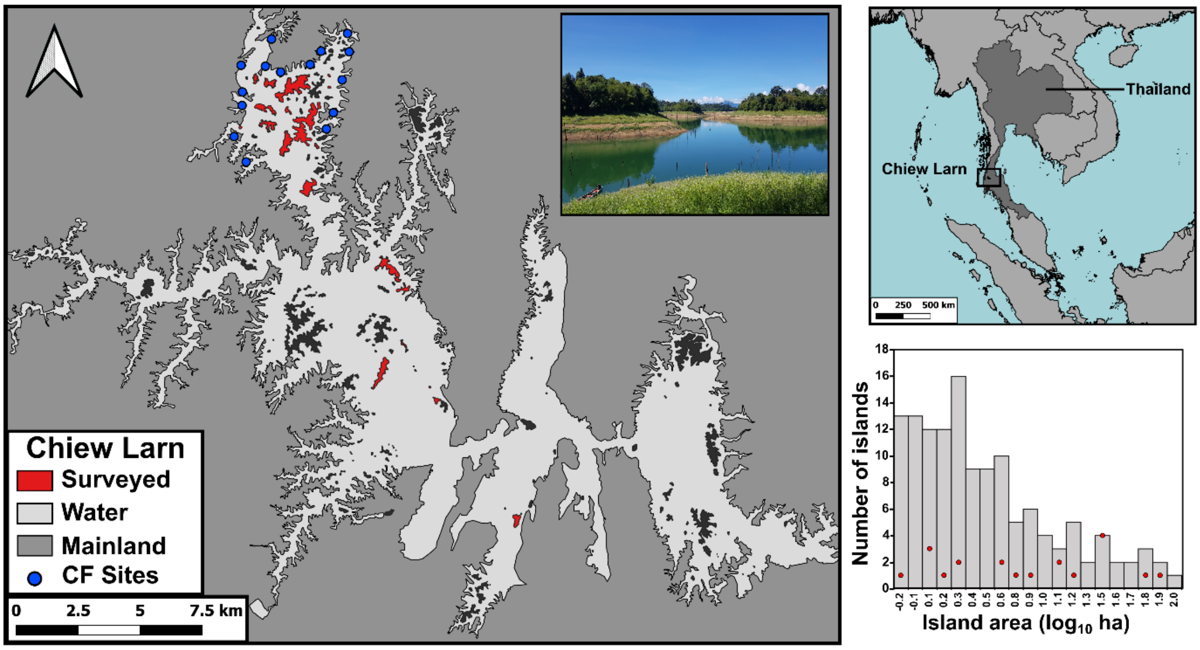


Figure 2.1. Map of Chiew Larn reservoir in Surat Thani province, Thailand (9°07'35.9"N, 98°37'24.2"E), showing surveyed islands (red) and the overall island size distribution (red points indicating surveyed islands).

Small mammal surveys

Small mammal assemblages were surveyed during three sampling periods: 12 islands from t_1 (3 surveys), 16 islands (12 resampled from t_1) from t_2 (2 surveys), and 20 islands (15 resampled from t_2, 12 resampled from t_1) in t_3 (1 survey). Island sizes ranged from 0.3 to 63 ha. Abundance was standardized to number of individuals per single transect by dividing total abundance by the sampling effort (number of transects) per island per year

(Table S2.1). Small terrestrial mammals were surveyed using a combination of Sherman (10 x 8 x 30.5 cm) and Tomahawk (14 x 14 x 41 cm) live traps arranged along transects. The number of transects per island was proportional to island area (Schoereder et al., 2004), with one transect on islands <20 ha, two transects on islands 20-40 ha, and 3 transects on islands >50 ha. I also surveyed three continuous forest (CF) sites, deploying 5 transects at each site >500 m from the reservoir edge. Each transect consisted of 10 trap-stations, each station separated by 15 m. At each station, I placed one Tomahawk trap on the ground and one Sherman trap within the understory vegetation, attached to lianas or tree trunks, to sample both terrestrial and arboreal species. Traps were baited using a combination of bananas, oats and peanut butter, and monitored for 5 consecutive nights, checked and re-baited every 24 hours. Captured individuals were identified using Francis (2008), sexed and measured for body weight, body length, and tail length. All field methods in the most recent surveys were consistent with previous surveys [6-7]. All individuals were marked using ear tags and released unharmed following the guidelines approved by the American Society of Mammologists (Sikes et al., 2019).

Environmental and biological variables

The following environmental variables were examined to test their effect on the diversity of the small mammal assemblage persisting within the fragmented landscape: island area ($\log_{10}$ x), shape index calculated as (Perimeter / (2 * SquareRoot(PI * Area)) and island perimeter length, distance to mainland, isolation time (yrs), and Normalized Difference Vegetation Index (NDVI). The % dominance of *Rattus tiomanicus* was also included as a covariate. Variance inflation factor (VIF) values were generated to indicate whether variables contained high collinearity, with an ideal value <2; I also checked for variable inter-correlation. This resulted in the exclusion of shape index and island perimeter length (Figure S2.1). All mapping and GIS layer manipulation was performed using QGIS version 3.16.4 (QGIS.org, 2023). Island sizes and distance to mainland were extracted using open street map data (OSM, 2020). NDVI was generated as an assessment of habitat quality, calculated using the QGIS raster calculator, by first subtracting the red band values from the near-infrared (NIR) bands, and then dividing this value by the sum of the red and NIR bands. Reflectance bands were extracted from Landsat 8 imagery. NDVI was calculated as the mean annual value, based on 12 months of Landsat 8 imagery from 2020, which was the year when the majority of the data was collected. This method was employed to minimize the variation in productivity or forest seasonality that might arise if Landsat 8 imagery from a single month was used to generate NDVI values.

Data analysis

Data analysis was conducted using R (R Core Team, 2023), including the packages "Cairo", "ggplot2", "corrplot", and "HH". Generalized Linear Models (GLMs) were used to examine the patterns of species persistence over time, using island area ($\log_{10}$) per survey period to predict species richness and abundance. Data from 1992-94 and 2012-2013 were modeled separately focusing on island size and proportional *Rattus tiomanicus* abundance as primary predictors of species richness. Species richness data from 2020 was extremely low for all islands, due to the monodominance of *R. tiomanicus,* so analysis could not be performed. The relationship between island size and proportional *R. tiomanicus* abundance was estimated using linear models for each year and projected to all unsurveyed islands to depict the increasing dominance of *R. tiomanicus* over time (Figure S2.2).

I then used piecewise Structural Equation Modeling (SEM) to disentangle the direct environmental effects from the indirect effects as mediated by *R. tiomanicus* driving small mammal species richness and abundance. The piecewiseSEM R package was used to generate SEMs (Lefcheck, 2016). Piecewise SEMs are a form of path analysis which test causal relationships between dependent and response variables (Shipley, 2000). This allows for testing and quantifying indirect effects that can be missed by any single model (Grace et al., 2007)**.** Path diagrams were converted into a set of linear equations, which were evaluated separately, allowing for smaller sample sizes to be analyzed (Lefcheck, 2016). Three path diagrams were designed to represent direct, indirect and a combination of direct and indirect effects combined on either native species richness or abundance; these were then compiled into three SEMs, which consisted of one Generalized Linear Mixed Model (GLMM) with either only direct (environmental) or indirect (% *R. tiomanicus*) variables or a combination of the two and a comparable GLMM. "Island" identity was included as a random effect to account for the 20 different islands sampled during t_1, t_2 and t_3.

The goodness-of-fit for the SEMs was assessed using Shipley's test of direct separation, determining if there are any missing relationships among unconnected variables (Shipley, 2000). The basis set constitutes a set of all potential relationships among unconnected variables in a path diagram (i.e. conditional independence). Shipley's test is performed by combining all *P* values for the basis set to produce a test statistic, Fisher's C. To avoid a saturated model which would prevent assessment of the goodness-of-fit, NDVI provided the smallest effect and was removed from the *R. tiomanicus* dominance linear model to prevent model saturation when running SEM analysis. An Akaike's information criterion value adjusted to small sample sizes (AIC_c) was also obtained using the Fisher's C statistic (Shipley, 2013), and I ordered each of the three SEMs (direct, indirect, and both) based on AIC_c values to evaluate model fit, the lowest AIC_c number indicating the best fit model, given that piecewise SEM assumptions are met. Models with ΔAIC_c values <3 were defined as providing substantial support, >3 and <7 were considered as moderately supportive, and >10 providing little to no support relative to the model set.

Results

Native small mammal richness declines

My 33-year dataset demonstrated a dramatic decrease in the total (and average ± standard deviation) number of species on islands, from 12 (4.08 ± 3.82) to 6 (1.75 ± 1.06) to 3 (1.10 ± 0.31), in (t_1, 1992-94 = 5-7 years; t_2, 2012-13 = 25-26 years; and t_3, 2020 = 33 years post-isolation), respectively. Mainland continuous forest (CF) richness in t_3, with 6 (3.30 ± 0.47) species, was twice as high as islands in t_3 but 50% lower than the species richness observed in t_1. Species-area relationships (SAR) over sequential sampling periods revealed a strong positive effect of island area in t_1 ($t = 5.63$, $P < 0.001$), a marginal effect in t_2 ($t = 2.93$, $P < 0.01$) and no effect in t_3 ($t = 0.94$, $P > 0.05$), demonstrating the complete collapse of the SAR due to the monodominance of *Rattus tiomanicus* (Figure 2.2; Table S2.2). Additionally, two squirrel and one treeshrew species had been detected in t_1 and t_2, while no such species were detected by t_3.

Changes in native small mammal and *Rattus tiomanicus* abundance

Over 33-years, I observed a slight increase in the average small mammal abundance per island over time, which became progressively dominated by the hyper-abundant *R. tiomanicus*, increasing from 7.95 ± 3.80 individuals (t_1) to 8.85 ± 7.10 individuals (t_3). The 2020 mainland CF average abundance (6.00 ± 2.80 individuals) was lower than that on islands (Figure 2.2). Focusing on *R. tiomanicus* only, I saw a 62% increase in average abundance per island from t_1 (5.33 ± 3.07 individuals) to t_3 (8.56 ± 7.49 individuals), which was 3.4 times higher than CF average abundance (2.47 ± 2.50 individuals).

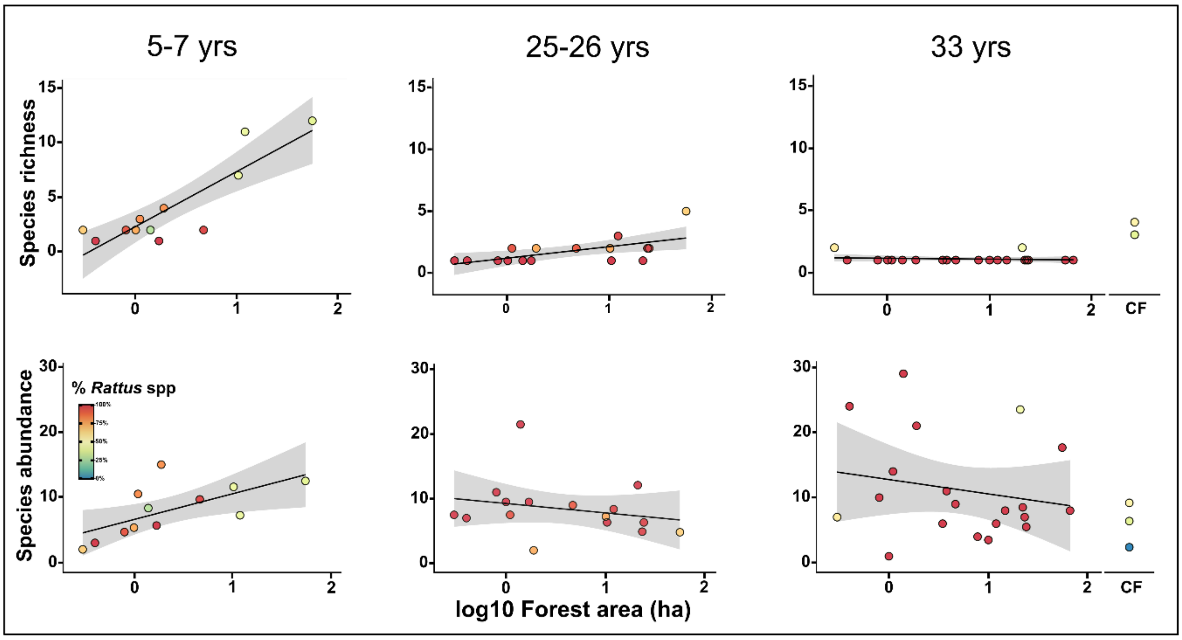


Figure 2.2. Species richness (top) and overall abundance (bottom) vs. island forest area (log_{10}) over time, 5-7 years (t_1), 25-26 years (t_2) and 33 years (t_3) post isolation. Each point represents one island fragment with three mainland continuous forest (CF) control sites in the final survey; points are colour-coded according to the percentage of all individuals represented by *Rattus tiomanicus*. Regression lines (black) with 95% confidence intervals (grey) are highlighted (see Figure S2.3 for a version of Figure 2.2 using only data for the 12 islands that were resampled over all three time periods).

Overall, the most abundant non-*Rattus* species in t_1 were the arboreal Indomalayan pencil-tailed tree mouse *Chiropodomys gliroides* ($N = 11.5$, 12.1% of the records) and the common treeshrew *Tupaia glis* ($N = 5$, 5.4%); combined, native species amounted to 34.0% of the captures in t_1. The proportional abundance of non-*Rattus* species on islands declined to 4.2% and 3.4% by t_2 and t_3, respectively, and neither squirrels nor treeshrews were detected by t_3. Over the sequential sampling periods, I report a significant positive relationship between species abundance and island area in t_1 ($t = 2.704$, $P = 0.022$). However, no such relationship was found for t_2 or t_3, although there was a trend towards higher abundance on smaller islands ($t = -1.341$, $P = 0.196$) as driven by *R. tiomanicus* dominance (Figure 2.2; Table S2.2). In fact, in contrast to other species, *R. tiomanicus* was the most abundant species during all survey periods and increasing in proportional abundance over time: from 66.0% (t_1) to 96.6% (t_3). This species initially became hyper-abundant on smaller islands in t_1, before reaching monodominance on all islands regardless of size by 2020 (Figure S2.1). A model averaging approach predicting the percentage of *R. tiomanicus* across all survey periods revealed a negative relationship with island size

($\log_{10}$) (z = 2.369, P = 0.018) and a positive relationship with time since isolation (z = 4.438, P <0.001) (Tables S2.3 and S2.4).

Native species richness and abundance responses to *Rattus* hyper-abundance

SEM analysis demonstrated that the primary drivers of altered local species richness were a combination of direct environmental effects, including a positive relationship with island area and NDVI and a negative relationship with isolation time, and indirect effects, including a negative effect of the magnitude of *R. tiomanicus* dominance (Table 2.1 and Figure 2.3). Increasing *R. tiomanicus* dominance was best explained by environmental effects, with a negative relationship with island area and a positive relationship with isolation time. The direct effect of distance to mainland on species richness and *R. tiomanicus* abundance was not significant (Figure 2.3). SEM analysis revealed that the primary predictors of species abundance declines were a combination of a direct environmental effect, a negative relationship with distance to mainland, and a strong negative relationship with *R. tiomanicus* dominance (Table 2.1 and Figure 2.3). The direct environmental effects of island area, NDVI and isolation time had no significant effect on species abundance.

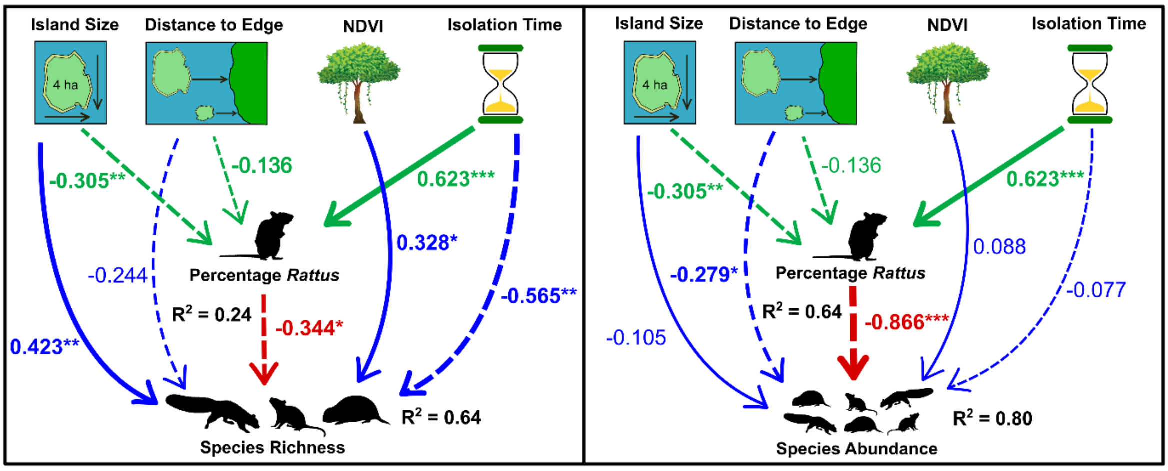


Figure 2.3. "Best" Structural Equation Models (SEMs) predicting species richness (12, 16 and 20 islands in t_1, t_2, and t_3, respectively) and abundance (12, 16 and 20 islands) across three time periods with direct environmental effects, including island size (ha), distance to mainland (m), Normalized Difference Vegetation Index (NDVI), and isolation time, and indirect effects, percentage of *Rattus tiomanicus*. Standardized coefficients are presented for each relationship, with solid and dashed lines indicating positive and negative relationships, respectively. Dark blue lines indicate direct environmental effects on richness; green lines indicate direct environmental effects on % *Rattus* dominance and the red line indicates direct effects of *R. tiomanicus* abundance on overall species richness and

abundance. Asterisks indicate the level of significance for relationships (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$) with a coefficient of determination (R^2) for each response variable. Line thickness is scaled to represent relative strength of effects. NDVI was not included as link to percentage *Rattus* within the SEM model due to prior assessment showing little importance (see table S2.3).

Table 2.1. SEM model best fit criteria for direct and indirect effects on species richness and abundance. With Fishers test C, *P* value and ΔAIC_c (Lowest ΔAIC_c number indicates the best fit model, given that piecewise SEM assumptions are met).

Model	***C***	***P***	**df**	**ΔAICc**
Species richness (*N* = 48)				
Direct*	54.071	0	4	3.783
Indirect*	18.849	0.004	6	15.967
Direct and indirect	3.42	0.181	2	0.000
Species abundance (*N* = 48)				
Direct*	118.153	0	4	159.754
Indirect*	18.157	0.006	6	0.000
Direct and indirect	3.420	0.181	2	1.042

Notes: SEMs built to identify the primary candidate model predicting species richness (*N* = 12, 16 and 20 islands in t_1, t_2, t_3 respectively) and species abundance (*N* = 12, 16 and 20 islands) over the three sampling periods. SEMs were split into direct effects (island area, NDVI, distance to mainland, years isolated), indirect effects (% *Rattus* dominance) and combining both direct and indirect effects. All SEM models were fitted with Poisson distribution. C stats, *P* values and degrees freedom (df) relate to the Fisher test which is used to determine if there are non-random associations between variables. The Akaike information criterion adjusted for small sample sizes (AIC_c) was used to measure model fit. ΔAIC_c was subsequently calculated with the lowest number indicating the best fit model, given that piecewise SEM assumptions are met (highlighted in bold typeface). * indicates piecewise SEM assumptions not met for the model from the Fisher test.

Discussion

Using a 33-year dataset following the trajectory of a small mammal community post isolation, I demonstrate a dramatic decrease in the richness and abundance of species on islands over time, leading to the complete collapse of the species area relationship, a fundamental pattern in ecology (Lomolino, 2000a). Simultaneously during this 33-year period of isolation I also document a substantial increase in *R. tiomanicus* abundance over time, subsequently dominating the entire fragmented insular landscape. I then tested which variables were driving the observed trends of species richness and abundance declines and increasing *R. tiomanicus* dominance. I found several direct environmental effects driving richness declines including a positive effect of island area, a key component of the ETIB framework (MacArthur & Wilson, 1967), along with a positive effect of habitat degradation (NDVI) and a negative effect of isolation time, while the only direct environmental effect driving species abundance was isolation distance. The results also revealed the main drivers of *R. tiomanicus* dominance with a negative effect of island area and a positive effect of isolation time. This dominance of *R. tiomanicus* was a significant driver of both richness and abundance declines, providing a strong negative effect.

In light of the negative impact *R. tiomanicus* is having on both species richness and abundance, the primary traits likely accounting for these species' declines are aggression and body size, as larger and more aggressive species are generally competitively superior to smaller and less aggressive species (Persson, 1985). For example, in New Zealand the larger brown rat *Rattus norvegicus* outcompetes the smaller black rat *Rattus rattus* through direct conflict (King, Foster, et al., 2011), while the black rat in turn is able to directly outcompete the smaller Polynesian rat *Rattus exulans* (Russell et al., 2015). Additional traits potentially contributing to species declines might include narrow niche breadths (Slatyer et al., 2013), whereby dietary and habitat specialists are at higher risk of extinction(Chichorro et al., 2019; Clavel et al., 2011; McKinney & Lockwood, 1999) and predisposed to limited dispersal capabilities which prevents recolonization from source populations (Brunke et al., 2019; Henle et al., 2004). It is possible that the observed reduction in richness within CF sites compared to t_1 is due to a combination of edge effects and increasing habitat degradation, paralleling some of the conditions present on islands, thereby decreasing native species richness while allowing *Rattus* dominance to increase.

Crucially, I found that the extent and rate at which species richness declined on Chiew Larn islands far exceeded that of other community-wide small mammal studies worldwide within island fragments. I compiled analogous studies from a global review on extinction debts (Jones et al., 2016) along with additional literature searches (Granjon et al., 2002;

Palmeirim et al., 2018) and found that no previous study had demonstrated the complete dominance by a single species, as seen at Chiew Larn. In fact, my 2020 results revealed a collapse of species richness 7 years faster than the theoretical prediction of complete relaxation to monodominance which was derived from the same study landscape [7].

R. tiomanicus became monodominant throughout the entire landscape, while other native species populations crashed. Initially, in t_1, the two most arboreal species were best able to escape *Rattus* dominance, while more terrestrial species declined rapidly likely due to more intense competition with *Rattus*. However, over time these arboreal species eventually disappeared, likely due to sustained competition with *Rattus* combined with their highly limited aquatic dispersal abilities (Brunke et al., 2019), which prevented further recolonization from source populations. *Rattus* spp. only require a small number of founder individuals to establish an insular population and can breed year-round depending on resource constraints or density-dependent effects (Harper & Bunbury, 2015). It is possible that as islands became more degraded over time from edge effects, pioneer plant species such as bamboo increased, potentially providing additional nesting sites. Bamboo fruiting has also been linked to population irruptions in *Rattus* spp. (Htwe et al., 2010). *Rattus* spp. also bear many traits ideal for exploiting increasingly degraded habitats, for example, using highly opportunistic foraging strategies, with broad diets consisting primarily of plant material, insects and terrestrial crustaceans (Riofrío-Lazo & Páez-Rosas, 2015); furthermore, the overlap in dietary requirements with co-occurring species such as murid rodents and tupaiids could have contributed towards their declines (Langham, 1983). Although *Rattus* spp. behave as ground and understorey habitat generalists, they are highly adept climbers that indiscriminately use the three-dimensional forest structure(Loveridge et al., 2016), unlike native species whose movement patterns are negatively impacted by altered forest structure (Cusack, Wearn, et al., 2015; Wells et al., 2004, 2006). Similar to other murid rodents, *Rattus* spp. also exhibit high dispersal capacity in traversing the inhospitable open-water matrix (Russell et al., 2005; Santori et al., 2008). I recorded 10 events of *R. tiomanicus* traversing between transects (separated by a minimum distance of 500 m), with one 860-m dispersal event swimming between different islands and a second >1.7-km event swimming from an island to a mainland CF transect. I also directly observed three separate events of *R. tiomanicus* actively swimming between islands (JHM, personal observation). This proficient dispersal ability likely contributed to *Rattus* population expansion ensuring island colonization and migration during times of food shortage to relieve density-dependent effects. Alongside several additional factors such as aggressiveness, size-mediated dominance, loss of native predators, and increased habitat degradation on island fragments, these traits helped to ensure that *R. tiomanicus* became ubiquitous throughout the Chiew Larn archipelago.

This high dispersal capability demonstrated by *R. tiomanicus* has implications in terms of metapopulation ecology (Hanski, 1999), defined as a “population of populations” where by local populations which occupy habitat patches are interconnected by occasional movement of individuals between patches. The ability of these rats to move between different habitat patches allows for a dynamic exchange of individuals, making populations more resilient to environmental fluctuations, as it aids in the restoration of diminished or extinct populations and improves geneflow which maintains genetic diversity (Crespo-Miguel et al., 2022; Hanski & Gyllenberg, 1993). This dispersal factor could be just as important as the habitat quality of the island itself for contributing to the occurrence and hyperabundance of *R. tiomanicus*. Furthermore, there is the possibility that islands could be a net negative for conservation by subsequently providing a source population of invasive *R. tiomanicus* to the mainland leading to potential future declines in native fauna.

In light of the high dispersal capabilities of *R. tiomanicus,* it’s possible that the distance to mainland covariate, often used in island biogeography models as a measure of isolation, was too crude to demonstrate an effect in archipelagos of islands in close proximity to each other. Other covariates that may better explain isolation could include the proximity of an island to neighbouring islands using metrics like the nearest neighbour distance or average distance to other islands (demonstrating connectiveness). Alternatively, a network-based approach to model connectivity among islands could also be used to account for potential dispersal routes and identify well-connected versus isolated islands, although as matrix quality is equally inhospitable this may not be the most effective technique. Additionally, species dispersal capabilities, based on species traits, could also be incorporated to estimate isolation based on matrix type. In summary, a multifaceted approach that combines the covariates of proximity, network modelling, and species traits could better capture isolation dynamics in fragmented insular landscapes.

Invasion ecology considers the mechanisms facilitating the establishment, spread and subsequent impacts of a non-native species (Lockwood et al., 2013). My results indicate that the highest populations of *R. tiomanicus* were initially present on smaller islands in t_1, which were predominantly more degraded, then increased in number on larger islands as the habitat structure of larger islands also degraded over time. *R. tiomanicus* therefore benefited from the changing habitat conditions that ultimately contributed to the suppression of other native species. There are three main potential forms of competition between *R. tiomanicus* and other native species that could explain my results. The primary form likely explaining most observed trends is ‘interference competition’, in which direct agonistic interactions between native and invasive species can prevent access to common resources and territories resulting in declines and ultimately extinction of native species(Amarasekare, 2002). Interference competition has often been observed between *Rattus* spp. and native rodents (Harris & Macdonald, 2007; Stokes et al., 2009), with dominance through direct physical contest and aggression often favouring larger-bodied species(Persson, 1985). This may in part explain the continued, although declining, presence of Müller’s rat *Sundamys muelleri* detected on two Chiew Larn islands in 2020, down from 6 islands in 1994, while all other smaller bodied species had been extirpated.

A second form of competition known as ‘exploitation competition’ may also be contributing to the observed results, in which native species are indirectly negatively affected by an invasive species through competition for common resources such as food and nesting sites. Previous work on the dietary composition of rodents within an artificial island archipelago demonstrated that interspecific dietary overlap increases on islands, leading to more intense competition for resources between species (J. Wang et al., 2010). This is likely due to changes in available resources on islands, as mean seed sizes have been found to decline on smaller island fragments (Liu, Slik, et al., 2019). As *Rattus* spp. are proficient climbers that can utilise all levels of forest strata (Harris & Macdonald, 2007; Loveridge et al., 2016), this mobility allows them to indirectly outcompete native species whose movements are often inhibited by increasingly degraded landscapes(Cusack, Wearn, et al., 2015; Wells et al., 2006) limiting their access to food resources and nesting sites. However, as no direct behavioural interactions were recorded during the 33-year dataset, no definitive assessment can be made regarding whether *Rattus* is outcompeting native species through either ‘interference’ or ‘exploitation’ competition.

A third form of competition possibly contributing to some of the observed trends is ‘apparent competition’, which occurs when native mesopredator abundance increases due to a prey surplus, indirectly suppressing native species through elevated predation levels (Hanna & Cardillo, 2014; A. P. Smith & Quin, 1996). *Rattus* may be supplementing that prey surplus, but continue to dominate the landscape due to their rapid reproductive capacity while other native species decline (Harper & Bunbury, 2015). An alternative explanation for increases in mesopredator abundance is ‘mesopredator release’, which occurs when apex predators, which normally regulate mesopredator populations, decline due to fragmentation effects(Conner & Morris, 2015; Prugh et al., 2009; Ritchie & Johnson, 2009). Contrastingly, the ‘predator mediated co-existence hypothesis’ suggests that predators are critical in maintaining prey diversity by controlling highly competitive species within the community; consequently, when predators are lost due to fragmentation, prey diversity may decline as hyper competitive generalist species take over (Estes et al., 2011; Henke & Bryant, 1999). To address these three theories surrounding mesopredator abundance I evaluated data from 27 camera traps on islands, amounting to 1,159 trap nights and >28,800 photos. I detected two mammalian mesopredators on islands, four independent captures of the golden cat *Catopuma temminckii* with a relative abundance index (RAI) of 0.34 and one capture of the common palm civet *Paradoxurus hermaphroditus* with a RAI of 0.07. Independent captures are defined as images taken more than 30 minutes apart, while RAI is defined as the number of independent captures per 100 trap nights (O'Brien et al., 2003). In comparison, work performed within the mainland of the Khlong Saeng –Khao Sok Forest Complex (Petersen et al., 2020) found the RAI of golden cats to be 3x higher at 1.08, while common palm civets had a similar RAI at 0.09. In addition, of the nine mesopredator species detected in the mainland forest study, only two were detected on islands suggesting that mesopredators are limited within insular areas potentially contributing to *Rattus* proliferation.

Implications for ETIB and extinction debt

Despite a lack of clarity of the key mechanisms driving the full establishment and consequential dominance of *R. tiomanicus* populations across the Chiew Larn archipelago over three decades, their proliferation represents a departure from the main tenets of island biogeography theory (MacArthur & Wilson, 1963; Preston, 1962), which expresses a simpler equilibrium of species richness balanced by a combination of local extinctions and immigration of new species. *Rattus* hyper-abundance also accelerated the rate at which 'extinction debts' were paid. My results indicate that *R. tiomanicus* has a strong detrimental effect on small mammal species richness, to the point of neutralizing the species-area relationship (Figure 2.2; Figure 2.3), with *Rattus* monodominance elevating local competitive conditions and subsequently preventing the re-establishment of local species from source populations. Examples of *Rattus* impacting ETIB and 'extinction debts' are limited within the literature and consequently my results here provide important insights into how *Rattus* spp. can decimate faunal assemblages in insular fragmented forest habitats, serving as a warning to other landscapes that are yet to experience a *Rattus* invasion.

Implications to conservation management

The hyper-abundance of an invasive rodent in insular fragmented forest landscapes threatens not only the diversity of small mammals but also that of birds (Jones et al., 2016), reptiles (Case & Bolger, 1991), invertebrates (Towns et al., 2006) and plants (McConkey et al., 2003). These taxa have all been documented as impacted by *Rattus* spp. invasions on true islands (Harper & Bunbury, 2015; Harris, 2009), and on insular forest fragments could also suffer shifts in community structure as part of an ecosystem-wide ecological meltdown (Terborgh et al., 2001). Local human communities may also be affected by elevated abundances of *R. tiomanicus*, which are potential vectors for diseases such as leptospirosis (Azhari et al., 2018), and through economic damage caused by crop raiding (Wood & Fee, 2003).

The key management recommendation to suppress *Rattus* populations would be to prevent landscape fragmentation in the first place as these rodents are human-commensals and are less likely to proliferate within large tracts of undisturbed primary forest (Nakagawa et al., 2006; Stokes et al., 2009; Wells et al., 2014). Previous studies in other archipelagic landscapes also suggest that retaining forest patches larger than 475 ha can support species-rich vertebrate communities containing ≥80% of the local fauna (Benchimol & Peres, 2015b). Maintaining >40% forest cover at the landscape scale and a high-quality matrix between patches would further ensure a nearly full complement of species (Arroyo-Rodríguez et al., 2020; Gillies & St. Clair, 2008). Direct control or eradication of invasive *Rattus* populations using techniques such as poisoning (anticoagulants) and trapping (Capizzi et al., 2014) has been attempted but often fails due to the 'sink effect' with rapid reinvasions from wider meta-populations (King, Innes, et al., 2011; Russell et al., 2005).

Conclusion

My results suggest that *Rattus* hyperabundance in fragmented insular landscapes could be playing a role in accelerating the rate at which species are lost, faster than that expected by the ETIB alone. Once *Rattus* secures a foothold, local competitive conditions simply become too hostile for native populations to become re-established. I found that virtually the entire native small mammal fauna can be lost in a tropical archipelagic landscape within three decades, illustrating the short timeframe at which an extinction debt can be paid in extreme conditions. Although this study is limited in identifying the primary mechanisms leading to *Rattus* monodominance, the potent combination of favourable species traits such as increased aggressiveness, larger body size and high dispersal capacity, alongside elevated habitat degradation and reductions in native predators on island fragments, all likely contributed to its proliferation throughout the landscape. This study indicates that small mammal assemblages are likely to vanish from other small island fragments (<100 ha), especially those overrun by invasive species and experiencing limited connectivity demonstrating the devastating effects of dam construction on native fauna. This also forewarns the potential for *Rattus* invasions throughout other insular fragmented landscapes both in Southeast Asia, Africa and the Neotropics, as native species' impacts on co-occurring species can be a good predictor of future invasiveness outside their native range (Capizzi et al., 2014; Filgueiras et al., 2021). Conservation efforts should focus on retaining and restoring large tracts of continuous forest landscapes to maintain stable and ecologically balanced faunal assemblages.

Chapter 3 : Degraded landscapes dominated by hyperabundant generalist mammals undermine the species-area relationship

Abstract

The species-area relationship (SAR) is a fundamental pattern found in nature, yet our understanding of the effects of habitat quality on the predictive power of SARs is limited. To address this, I examined three landscapes of island fragments isolated within hydroelectric reservoirs in Southeast Asia, spanning a gradient of habitat disturbance. This disturbance was measured using the normalized difference vegetation index (NDVI), declining between landscapes from (average ± SD) 0.378 (± 0.030), to 0.297 (± 0.038), to 0.230 (± 0.026), at Kenyir, Chiew Larn and Vajiralongkorn, respectively. I compared small mammal assemblages on islands of different sizes, isolation, and degree of degradation. I found that, as disturbance increased, the predictive power of SAR models declined from 43% to 4% and back to 22%, Kenyir, Chiew Larn and Vajiralongkorn, respectively. I also documented the collapse of the SAR at two of my study landscapes with only a single *Rattus* species persisting in my most degraded landscape (Vajiralongkorn) and community abundance declining by 96%. My results markedly diverge from traditional SAR patterns where island size is the primary predictor of species diversity. This study suggests that increased degradation in fragmented forest landscapes has both direct impacts on small mammal species richness as well as indirect effects by contributing to the proliferation of *Rattus*, which combine to override the species-area relationship. To limit these impacts, I suggest retaining large tracts of high-quality continuous forest to preserve the integrity of small mammal assemblages.

Introduction

The species-area relationship (SAR) is a fundamental principle in ecology that has provided valuable insights into biodiversity patterns and ecosystem dynamics (Lomolino, 2000a; MacArthur & Wilson, 1963). SARs describe the positive association between the size of a habitat and species diversity and have long served as a guiding tool for understanding patterns of biodiversity within habitat remnants (Lomolino, 2000a). SARs are a key component of the Equilibrium Theory of Island Biogeography (ETIB), which provides a model framework predicting species richness based on species immigration and extinction rates modulated by habitat area and isolation from mainland species pools (MacArthur & Wilson, 1963, 1967). Various SAR models exist but the two most observed forms are the power-law SAR, which suggests that species richness increases rapidly with increasing area initially but then levels off as saturation is reached, and the logarithmic model, which suggests a linear relationship on a logarithmic scale between species richness and habitat area. However, these traditional models assume an inherent correlation between habitat area and increased habitat quality, niche availability and resource availability (MacArthur & Wilson, 1967). This relationship has held true for countless ecological studies (Jones et al., 2016; Matthews et al., 2021) but despite a wealth of research and publications on SARs and the ETIB, little is known as to how landscape quality (Banks-Leite et al., 2020) can impact this ironclad rule in ecology (Matthews et al. 2014). This knowledge is important as SARs are often relied upon as an effective tool for predicting the residing species diversity and shaping conservation policy for the landscape and if inaccurate may lead to either over or under-representation of the true impacts occurring within a landscape (He & Hubbell, 2011; A. B. Smith, 2010).

Forest fragmentation has become increasingly severe globally with only <10% of remaining continental forest patches >10,000 ha in size (Taubert et al., 2018). Forest fragmentation triggers a myriad of biotic changes in the ecosystem due to edge effects, such as increased temperatures, exposure to wind, and desiccation (Fahrig, 2003; Haddad et al., 2015; Murcia, 1995). Subsequent abiotic changes often lead to alterations in plant communities, with many of the structural components of pristine forest habitats lost or shifting towards earlier successional systems characterized by shorter-lived, smaller tree species (Liu, Coomes, et al., 2019; Tabarelli et al., 2008; Zambrano et al., 2019). This degradation can then be compounded further by human-induced disturbances through activities such as logging, fire and cattle grazing (Barzan et al., 2021; Bowman et al., 2009; M. C. Hansen et al., 2013). As the climatic and vegetative features of the landscape change, forest specialists are exposed to harsh environmental conditions, often leading to population declines and, in some cases, local extinction (Filgueiras et al., 2021). This is in part due to sensitivity of functional traits that allow the species to interact with the environment, such as dietary and habitat specialization, but also due to competitive traits such as small body size, reduced aggression, and limited dispersal ability (Betts et al., 2017; Henle et al., 2004). However, such changes often occur with a time lag known as an “extinction debt,” whereby species are lost over several years or decades (Ewers & Didham, 2005; Newbold et al., 2014). These alterations in the structural complexity and quality of the available habitat pose significant challenges to traditional SAR models. To accurately understand and mitigate the impacts of habitat degradation on biodiversity, it is crucial to incorporate these complexities into ecological models and conservation strategies.

To address how tropical forest habitat degradation may impact the SAR I sampled the small mammal communities which consist of murids, shrews and squirrels. These species range in their sensitivity to environmental change, from forest specialists to hyper dominant generalists such as *Rattus* spp capable of proliferating within degraded landscapes compounding the decline of the small mammal community (J. H. Moore et al., 2022). I used a unique experimental setting provided by hydroelectric dams of which over 58,000 exist globally, supplying 70% of the world’s renewable energy (IHA et al., 2018). The creation of hydroelectric dams often involves the flooding of large tracts of forest, leaving a fragmented matrix of former forest hilltops of varying size and isolation (Jones et al., 2016). Small mammal communities are subsequently isolated within these insular forest remnants and are subject to changing habitat conditions, acting as experimental laboratories allowing for the understanding of the effects of habitat fragmentation over time, revealing how extinction debts unfold post-isolation (Gibson et al., 2013) and the resulting SAR. One interesting aspect to the reservoirs in Southeast Asia is that rodents from the *Rattus* genus contribute to boost the effects of habitat loss and fragmentation, often dominating small mammal communities (J. H. Moore et al., 2022). I selected three hydropower reservoirs in Southeast Asia that have been isolated for similar time periods 33-36 years, and long enough for extinction debts to be paid revealing the true impact of habitat fragmentation and degradation on small mammal communities. These three landscapes also exist across a gradient of disturbance, represented by normalized difference vegetation index (NDVI) measurements (Pettorelli et al., 2005) which assess vegetative health and density providing an indirect assessment of habitat quality. Each reservoir included a semi-pristine landscape (e.g., no logging nor hunting since the reservoir was created), a landscape with reduced structural complexity, potentially due to over grazing from native herbivores, and a landscape with heavy human-mediated degradation (e.g., including the presence of cattle and annual fires).

I hypothesize that habitat degradation causes a decline in the predictive power of SAR models, and consequently in the slope of the relationship within the fragmented landscapes. As such, species richness of small mammal species will decline as degradation increases, irrespectively of island size. As small mammals do not necessarily decrease in abundance in the aftermath of disturbance (Michał & Rafał, 2014), this hypothesis did not apply to species abundance, which was rather expected to show the opposite trend. Moreover, I further expected that habitat degradation will lead to the dominance of more generalist species within the ecosystem; and that the modulating effects of habitat degradation alongside the hyper dominance of generalist species will be important predictors of species richness and abundance.

Methods

Study locations

This study was undertaken in Southeast Asia which consists primarily of lowland tropical forests which are prone to the formation of islands following damming and flooding. Sampling was conducted at three landscapes: Kenyir Lake in Terengganu, Malaysia (geographic coordinates: 4.98, 102.64), Chiew Larn reservoir in Surat Thani, Thailand (9.12, 98.62) and Vajiralongkorn Dam in Kanchanaburi, Thailand (15.01, 98.53) (Figure 3.1). All three study landscapes were chosen for their similar landscape characteristics such as the large number of islands (100-400 per landscape), range in island size (0.6 – 1,428 ha), time since isolation ranging from 33 years (Kenyir and Chiew Larn) to 36 years (Vajiralongkorn) and a considerable overlap in faunal communities (57% of species found in all three landscapes and 85% found in two landscapes). Importantly, these three landscapes span a gradient in anthropogenic forest habitat disturbance (see Figure 3.1D), allowing for the comparison of faunal change relative to landscape degradation. Although all landscapes experienced logging during the creation of their dams, Kenyir remains the least degraded landscape with a relatively intact canopy and understorey, Chiew Larn has experienced declines in structural complexity of the understorey shifting towards increasing dominance of pioneer species, potentially to increases in native herbivore species and Vajiralongkorn is significantly degraded with the addition of human-mediated disturbances such as fires and livestock grazing.

Landscape descriptions

The Kenyir Lake landscape comprises of lowland and mid-elevation dipterocarp forest. It experiences an average annual rainfall of 2,700 mm to 4,000 mm (Qie et al., 2011). The region follows a seasonal pattern with wet and dry seasons spanning from November to April and May to October, respectively. The construction of the Kenyir Dam in 1986 flooded over 2,600 km^2 of tropical forest habitat and resulted in the largest man-made lake in mainland Southeast Asia. This created >340 islands ranging in size from 0.6 to 1,428 ha. The reservoir borders Taman Negara National Park to the southeast, which I used as an reference continuous forest site.

The Chiew Larn landscape comprises a lowland monsoon evergreen forest with a mix of different successional stages. It experiences an average annual rainfall of 2,365 mm and mean annual temperatures of 26.8°C. The construction of the Rajjaprabha Dam in 1986 flooded 165 km^2 of forest within one year, resulting in the formation of more than 100 islands, varying in size from <1 ha to >100 ha. The forest surrounding the reservoir is divided between two protected areas: Khao Sok National Park (739 km^2), and Khlong Saeng Wildlife Sanctuary (1,155 km²), established in 1974, which serves as a control site of continuous forest habitat.

The landscape at Vajiralongkorn consists of mixed deciduous, hill evergreen and dry evergreen forest. The region experiences a rainy season (June to October), a cold season (November to January), and a hot season (February to May). On average annual rainfall for the region is between 1,600 and 2,200mm with mean annual temperatures of 21.0°C. The construction of the Vajiralongkorn Dam was completed in 1984, inundating 388 km^2 of forest and creating >400 islands ranging in size from <1 ha to > 900 ha. Those islands and the surrounding continuous forest are contained within the Khao Laem National Park (1,497 km^2), created in 1987 and here serving as a control study site.

Small mammal surveys

I surveyed small mammal assemblages on a different number of islands from the three study landscapes: 18 islands (0.84 – 416 ha) at Kenyir, with a combined survey effort of 2,900 trap-nights; 20 islands (0.3 – 68 ha) at Chiew Larn, amounting to 2,600 trap-nights; and, 16 islands (0.97 – 350 ha) at Vajiralongkorn, amounting to 1,900 nights (Figure 3.1A-C). Small mammals were live-trapped along linear trapping transects. The number of transects allocated per island was proportional to island area (Schoereder et al., 2004); specifically, islands smaller than 20 ha were assigned one transect, islands ranging from 20 to 40 ha were allocated two transects, and islands larger than 50 ha were surveyed using three transects. In addition to the island surveys, three continuous forest (CF) sites were also surveyed at all three landscapes. Each CF site was surveyed using five transects, all of which located at least 500 m away from the reservoir edge. For all sites, each transect was comprised of 10 trap-stations, each of which spaced 15 m apart. At each station, two types of traps were deployed to capture both terrestrial and arboreal species. Specifically, one Tomahawk trap (14 x 14 x 41 cm) was positioned on the ground, while one Sherman trap (10 x 8 x 30.5 cm) was placed in the understorey vegetation, secured to lianas or tree trunks, this setup was alternated between consecutive stations. Transects were surveyed during five consecutive nights (Kenyir – surveyed in August to November 2019, Chiew Larn – surveyed in June to July 2020 and Vajiralongkorn – surveyed in March to April 2020).

Traps were baited using a combination of bananas, oats, and peanut butter, and checked and rebaited every 24 hours. All individual captures were then identified to species, using a field guides to the mammals of Southeast Asia (Francis, 2008). Sex was determined, and measurements of body weight, body length, and tail length were recorded. The field methods employed in the most recent surveys remained consistent with previous studies (Gibson et al., 2013; Lynam & Billick, 1999; J. H. Moore et al., 2022). All animals captured in this study were marked using numbered ear tags (model 1005-1, National Band & Tag Company) and released unharmed, adhering to the guidelines set by the American Society of Mammologists (Sikes et al., 2019). Hereafter, I use *Rattus* spp to refer to *Rattus tiomanicus*, which was found at both Kenyir and Chiew Larn (Gibson et al., 2013), and *Rattus rattus*, which was found at Huai Kha Khaeng (Walker & Rabinowitz, 1992), near Vajiralongkorn.

Environmental variables

This study investigated the influence of the following environmental variables: island area, distance to the mainland and Normalized Difference Vegetation Index (NDVI), an approximate representation of forest habitat quality (Pettorelli et al., 2005). NDVI was generated using the QGIS raster calculator, computed by subtracting the red band values from the near-infrared (NIR) bands and dividing the result by the sum of the red and NIR bands (Vermote et al., 2016). I then calculated the mean raster NDVI value for each island. Reflectance bands were extracted for this purpose from Landsat 8 imagery with a 30m resolution. NDVI was calculated as the mean annual value, based on 12 months of Landsat 8 imagery from 2020, which was the year when the majority of the data was collected. This method was employed to minimize the variation in productivity or forest seasonality that might arise if Landsat 8 imagery from a single month was used to generate NDVI values. Mean (± SD) NDVI per landscape was 0.378 (± 0.030), 0.297 (± 0.038) and 0.230 (± 0.026), at Kenyir, Chiew Larn and Vajiralongkorn, respectively, showing the gradient in disturbance that my study spans (Figure 3.1D). Welch two-samples t-tests showed that mean NDVI was significantly different between all three study landscapes: Kenyir vs Chiew Larn ($t = -7.23$, $df = 35.27$, $p < 0.001$), Chiew Larn vs Vajiralongkorn ($t = 6.19$, $df = 32.871$, $p < 0.001$) and Kenyir vs Vajiralongkorn ($t = 15.515$, $df = 31.93$, $p < 0.001$). Island size and distance to the mainland were extracted using open street map data (OSM, 2020). All mapping and GIS layer manipulation was performed using QGIS version 3.16.4 (QGIS.org, 2023). Additional variables indicative of the intensity of the edge effects such as the island shape index , here defined as (Perimeter / ($2 \times \sqrt{}\ (\pi \times$ Area)) (Ripple et al., 1991), and island perimeter length were excluded from the analysis due to their high collinearity, defined as any variables with >0.7 correlation. Proportion of *Rattus* spp, here defined as the percentage of individual captures (excluding recaptures) belonging to the *Rattus* genus, was also included as a variable.

Data analysis

To standardize the abundance of small mammals, the total abundance count was divided by the sampling effort, which I define as the number of transects conducted per island per year. Data analysis was conducted using R (R Core Team, 2023) including the packages “Cairo”, “ggplot2”, “corrplot”, and “HH”. A species-area relationship (SAR) was generated using the power model ($S = cA^z$) from the “sars” package for each study landscape to provide baseline performance for the predictive power of the island area variable used within SAR models in explaining species richness (Matthews et al., 2019). The power model was chosen as it one of the most widely used SAR models within the literature (Dengler, 2009) and performed better than the logarithmic model.

I ran model selection to understand additional meaningful predictors other than island size that might better explain the observed richness declines between study landscapes, including isolation distance, proportion of *Rattus* spp and habitat quality (Table S3.1, S3.2 and Figure S3.1). I then aimed to disentangle the role of habitat degradation from that of habitat loss and fragmentation. Given previous evidence on the role of *Rattus* spp. in driving species richness and abundance in one of the surveyed reservoirs (J. H. Moore et al., 2022), I also considered here the proportion of Rattus spp. I applied piecewise Structural Equation Modelling (SEM) using the SEM package (Lefcheck, 2016). Piecewise SEMs are a type of path analysis which allows to disentangle the direct environmental effects from the indirect effects triggered by *Rattus* spp dominance on small mammal richness and abundance, examining causal relationships between dependent and response variables (Shipley, 2000). Indirect effects are often overlooked by single models which SEM analysis can account for (Grace et al., 2007). By converting path diagrams into a set of linear equations, it became possible to assess them independently, enabling the analysis of smaller sample sizes (Lefcheck, 2016).

I designed three path diagrams to represent direct, indirect and a combination of direct and indirect effects on small mammal species richness; these were then compiled into three SEMs, which consisted of one Linear Mixed Model (LMM) with either only direct (environmental) variables, only indirect (% *Rattus* spp) variables, or a combination of the two. ‘‘Landscape’’ identity was included as a random effect to account for inherent variability between the three studied reservoirs.

To evaluate the goodness-of-fit of the structural equation models (SEMs), Shipley's test of direct separation was employed to identify any potential missing relationships between unconnected variables (Shipley, 2000). The basis set represents a collection of all possible relationships between unconnected variables within a path diagram, indicating their conditional independence. To conduct Shipley's test, the p-values for the basis set are combined to generate a test statistic known as Fisher's C. To ensure the assessment of goodness-of-fit in the SEM analysis, isolation distance, the variable with the smallest effect, was excluded from the linear mixed model to avoid model saturation. In order to assess model fit, I calculated the Akaike Information Criterion value adjusted for small sample sizes (AICc) using the Fisher's C statistic, as proposed by (Shipley, 2013). AICc values were obtained for each of the three SEMs (direct, indirect, and combined), and I ranked the models based on these AICc values. ΔAIC_c were subsequently calculated with the lowest value considered the best fit, assuming that the assumptions of piecewise SEM were met. Models with ΔAICc values less than 3 were considered to provide substantial support, while those with values greater than 3 and less than 7 were considered moderately supportive. Models with ΔAICc values exceeding 10 were deemed to provide little or no support to the model set (Shipley, 2013) (Table 3.1).

Ethics statement

All surveys in this study were carried out in accordance with regulations on animal ethics and other laws and approved by the National Research Council of Thailand (No. 0402/4356) and in line with the Malaysian code of practice for the care and use of animals for scientific purposes established by the animal welfare board, Department of Veterinary Services, Malaysia.

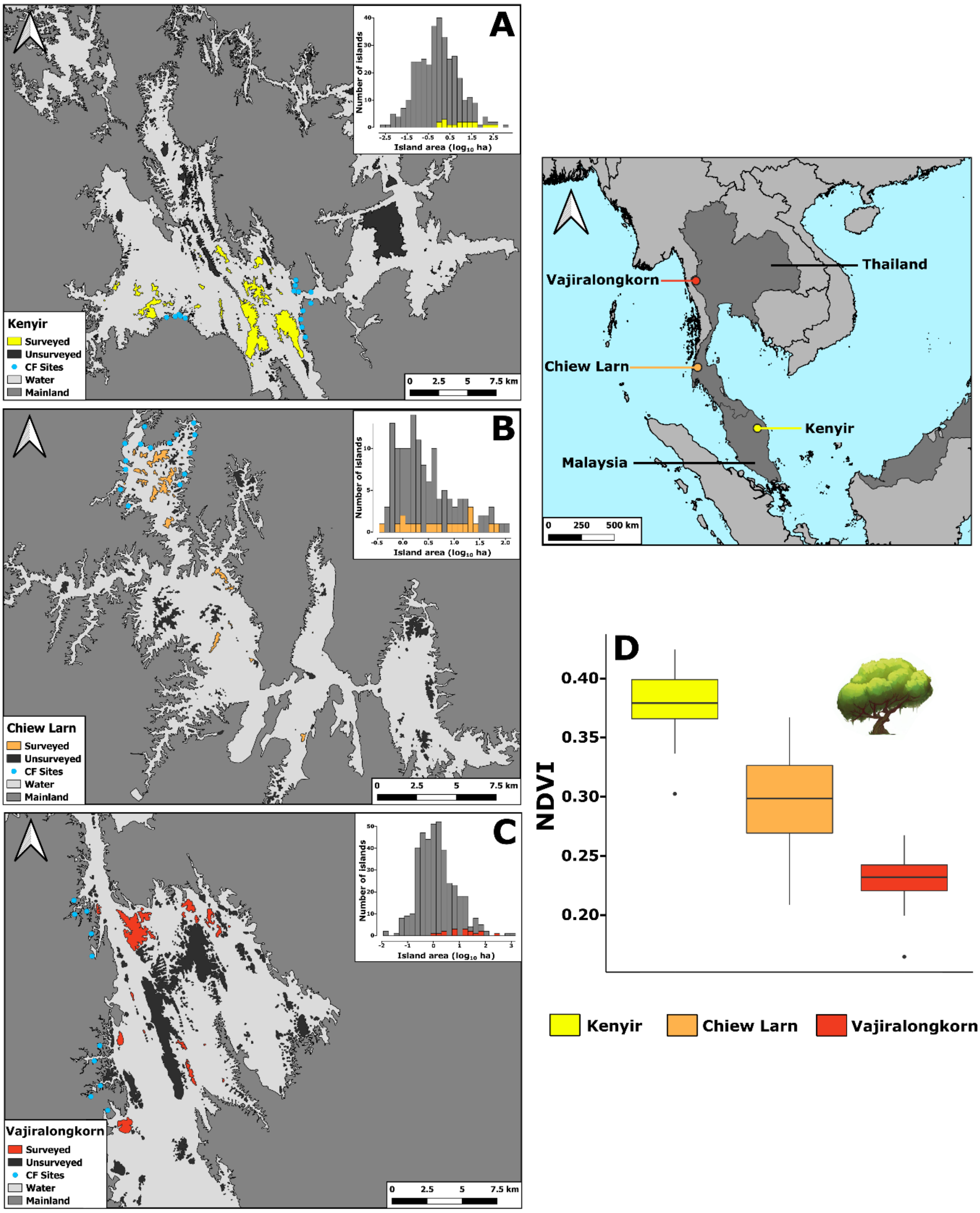


Figure 3.1. Study landscapes for (A) Kenyir, (B) Chiew Larn, and (C) Vajiralongkorn reservoirs with histograms of surveyed (coloured) and unsurveyed (gray) islands. (D) Boxplots for island NDVI values with outliers marked as black dots.

Results

Small mammal richness and abundance

A total of eight small mammal species were detected across all islands within my three fragmented landscapes. Seven species were from the Muridae family (rats), and one species was from the Sciuridae family (squirrels), with no detections of Tupaiidae (shrews). My dataset showed a dramatic decrease in the total (and average ± SD) number of small mammal species on islands in more degraded reservoirs with species richness declining from 8 (1.78 ± 1.08) to 3 (1.1 ± 0.3) to 2 (1 ± 0) at Kenyir, Chiew Larn and Vajiralongkorn, respectively.

Overall (and average ± SD) small mammal abundance for all species, excluding *Rattus* spp, showed a dramatic decrease from 27 individuals (3.1 ± 6.2) to 6 (0.3 ± 0.9) and 1 (0.06 ± 0.24), in Kenyir, Chiew Larn and Vajiralongkorn, respectively. This represents a 96.3% decline in overall small mammal abundance other than *Rattus* spp. between the most pristine landscape (Kenyir) and the most degraded landscape (Vajiralongkorn). Conversely, the abundance of *Rattus* spp increased by 103% between Kenyir (84 captures) and Chiew Larn (171 captures), but decreased to only 12 captures in Vajiralongkorn, which was 85.8% and 93% lower than at Kenyir and Chiew Larn, respectively. *Rattus* spp community dominance increased from 75.8% of all captures at Kenyir to 96.6% at Chiew Larn and 92.5% at Vajiralongkorn.

A significant species-area relationship, generated using the power model ($S = cA^z$), was present at Kenyir ($C = 1.061$, $Z = 0.198$, $p > 0.003$, $R^2 = 0.43$), the least degraded landscape. Any area effect has been completely collapsed at Chiew Larn ($C = 1.034$, $Z = 0.037$, $p = 0.375$, $R^2 = 0.05$), my second most degraded landscape. At the Vajiralongkorn, my most degraded landscape, area tended to exert a positive effect, although not significant ($C = 0.296$, $Z = 0.231$, $p = 0.088$, $R^2 = 0.22$), (Figure 3.2A-C).

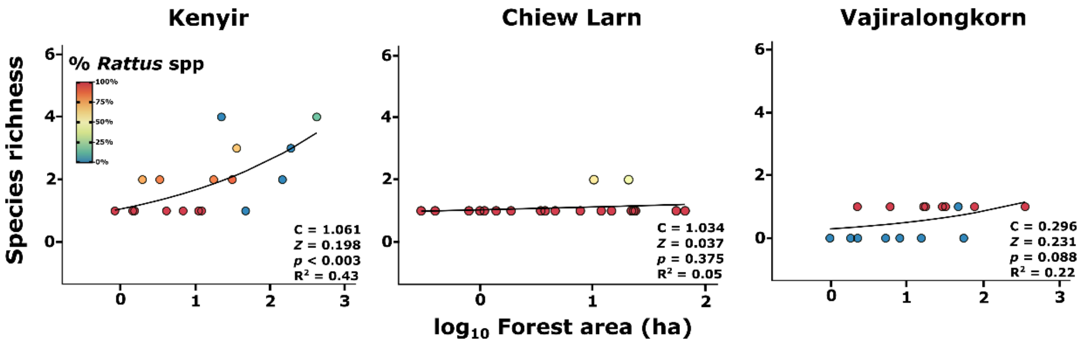


Figure 3.2. Species-area relationships (SAR) for small mammals at Kenyir, Chiew Larn and Vajiralongkorn. Sampling landscapes are color-coded according to the percentage of *Rattus* spp (%). The solid lines depict the best fit model as estimated using the SAR power model ($S = cA^z$).

Table 3.1. Structural equation model best-fit criteria examining direct and indirect effects on small mammal species richness and abundance. Fisher's test *C*, *p* value, and ΔAIC_c. Lowest ΔAIC_c number indicates the model with the best fit, given that piecewise SEM assumptions are met. *Denotes that piecewise SEM assumptions were not met for the model from a Fisher's test.

Model	***C***	***p***	**df**	**ΔAIC_c**
Species richness				
Direct*	33.754	0	4	18.234
Indirect*	16.064	0.003	4	0.000
Direct and indirect	5.125	0.077	2	3.709
Species abundance				
Direct*	12.628	0.013	4	0.639
Indirect	4.12	0.39	4	8.284
Direct and indirect	5.125	0.077	2	0.000

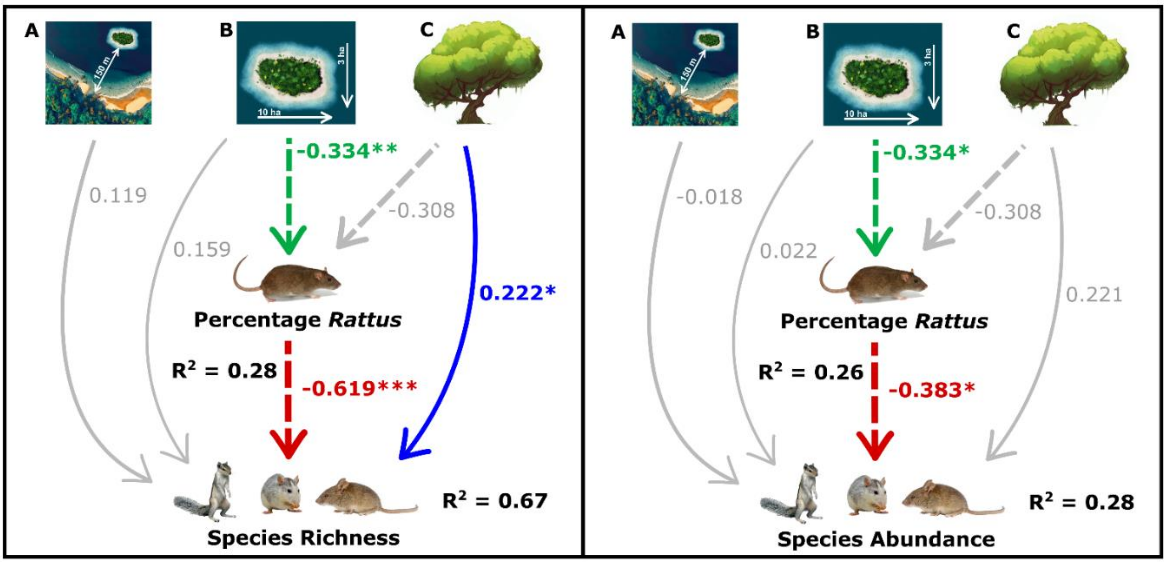


Figure 3.3. ‘‘Best” structural equation models (SEMs) predicting species richness and abundance across three landscapes of increasing degradation (considering 18, 20, and 16 islands sampled at Kenyir, Chiew Larn and Vajiralongkorn, respectively). Direct environmental effects, including (A) isolation distance (m), (B) $\log_{10}$ (island size) (ha) and (C) normalized difference vegetation index (NDVI), and an indirect effect, the proportion of *Rattus* spp captures. Standardized coefficients are presented for each relationship, with solid and dashed lines indicating positive and negative relationships, respectively. Dark blue lines indicate direct environmental effects on species richness; green lines indicate direct environmental effects on % *Rattus*, and the red line indicates direct effects of *Rattus* spp proportion on overall species richness (other than *Rattus*). Grey lines are non-significant effects. Asterisks indicate the level of significant relationships (*$p < 0.05$, **$p < 0.01$) with a coefficient of determination (R^2) for each response variable. Line thickness is scaled to represent the relative strength of effects.

Table 3.2. Examples of studies demonstrating a variety of anthropogenic stressors modulating species-area relationships for a variety of taxa.

Anthropogenic modulators	**Taxa**	**Reference**
Edge effects	🌳	(Benchimol & Peres, 2015a)
Edge effects	🐦 🦌	(Koh et al., 2010)
Habitat quality	🦋	(Öckinger & Smith, 2006)
Habitat quality	🌳	(Schrader et al., 2019)
Habitat quality	🦎	(Silva et al., 2022)
Habitat quality	🌳 🦋 🐀 🦎 🐦 🪲 🦇	(Triantis et al., 2003)
Hunting	🐒	(Benchimol & Peres, 2013)
Hunting	🐦	(Sreekar et al., 2015)
Invasive species	🐀	(J. H. Moore et al., 2022)
Matrix quality	🐒	(Benchimol & Peres, 2013)
Matrix quality	🐦	(Koh & Ghazoul, 2010)
Matrix quality	🦋	(Lizée et al., 2012)
Matrix quality	🐦 🦌	(Koh et al., 2010)

Taxonomic guide: 🦇 bats, 🪲 beetles, 🐦 birds, 🦋 butterflies, 🦌 large mammals, 🦎 lizards, 🌳 plants, 🐒 primates and 🐀 small mammals.

Discussion

Across the increasing overall habitat degradation gradient orderly characterizing each of the three reservoirs surveyed, I document the complete collapse of the species-area relationship. My results further demonstrate a remarkable departure from expectations based on the Equilibrium Theory of Island Biogeography. In fact, within my most habitat degraded landscape (Vajiralongkorn), I observe a partial but non-significant revival in the SAR, driven by the fact that even the hyper dominant *Rattus* species could not be retained on half of the islands. Besides *Rattus* spp., only a single species was detected in my most degraded landscape, Vajiralongkorn, compared to seven species in my highest quality landscape, Kenyir. Using structural equation modelling, I was able to unveil the fundamental role of habitat quality, directly predicting small mammal species richness but not abundance. As expected, the proportion of *Rattus* spp. increased at smaller forest sites and was also an important driver of both small mammal species richness or abundance.

The ETIB has been one of the most influential equilibrium models over the past 50 years in attempting to explain current patterns of biodiversity (MacArthur & Wilson 1963, 1967). ETIB is also phenomenologically related to the species-area relationship which is often seen as an ironclad “law” in ecology (Lomolino, 2000a; Rosenzweig, 1995). However, the appropriateness of model fits has come into question in recent decades as both island biogeographic models and SARs almost entirely overlook the effects of habitat quality along with other anthropogenic stressors, which are often assumed to be implicitly invariant. This is however not the case in an increasingly human modified world where environmental stressors may often interact (Haddad et al., 2015; Taubert et al., 2018; Tjørve, 2003, 2009). In fact, a study that examined 449 datasets with SAR power models in island ecosystems showed a large range in the R^2 value of island species-area relationship models averaging 0.64 (Triantis et al., 2012). In other words, 30-40% of the variation in species richness is often overlooked and can be explained by other external anthropogenic stressors such as habitat quality or hunting (Benchimol & Peres, 2013; Matthews et al., 2016; Triantis et al., 2012). Previous work also shows a weak effect size of island area when using standard SAR models to predict species richness within land-bridge islands (Neto et al., 2022). My work adds to a growing body of literature showing the importance of including different types of anthropogenic disturbance such as edge effects, logging, hunting, and invasive species in improving the predictive accuracy of SAR models across a variety of taxa (Table 3.2). To incorporate these factors into SAR models, additional terms could be added alongside the ‘area’ metric to account for these anthropogenic factors, producing GLMMs. These terms could represent the impact of different factors on biodiversity, such as a ‘hunting’ term or a ‘edge effects’ term. Researchers have turned to GLMMs to increase the explanatory power of their models as SARs alone are sometimes poor predictors of richness in a complex ecosystem, particularly when experiencing high anthropogenic impacts. Although this is a small sample of the available literature, it is clear that ecosystems are more complex in the way they respond to fragmentation than the traditional SAR and ETIB framework is capable of explaining.

Habitat degradation of remaining forest fragments has the potential to directly impact small mammal richness (but not abundance) in a multitude of ways. Habitat patches become increasingly degraded over time, largely due to edge effects altering microclimatic conditions and allowing increased solar radiation and wind exposure, leading to more desiccated, hotter environments (Benchimol & Peres, 2015b; Laurance, 2008). However this gradual form of disturbance alone does not explain the habitat degradation gradient that exists between sites which in Vajiralongkorn, the most degraded site, has been intensified by human-induced activities through processes such as burning which reduces both the structural complexity of the understory and regenerating capability (Bowman et al., 2009; Prestes et al., 2020), and cattle grazing which simplifies the understory structure, opening up the ground-layer and generating a higher proportion of bare ground (Barzan et al., 2021; Landsberg et al., 2003). The explanation for the increased degradation at Chiew Larn is more nuanced and may be due to the increased presence of natural herbivores over grazing the islands and impacting the regenerative capacity of the islands. This elevation in degradation cause abiotic changes which are hostile to many species, leading to declines in climatically sensitive species found in pristine closed-canopy forest habitats. Further physical damage can result from increased gusts of wind causing treefalls, branch breakages, and uprooting, further opening the canopy and exacerbating forest degradation (Laurance & Curran, 2008; Murcia, 1995). This results in a microclimate more favorable to pioneer species, such as bamboo, driving tropical forest fragments to an early successional stage (Liu, Coomes, et al., 2019; Tabarelli et al., 2008, 2012), depleting taller, longer-lived tree species, all of which are linked to a subsequent decay in structural complexity and niche availability.

As many species are habitat specialists with narrow niche breadths (Slatyer et al., 2013), a more degraded landscape can have direct consequences for persistence rates through a reduction in food availability and nesting habitat, and increased physiological stress from hotter and drier conditions (Chichorro et al., 2019; Clavel et al., 2011; Gibson et al., 2011; McKinney & Lockwood, 1999). Alterations in forest structure have also been documented to detrimentally impact native species movement patterns (Cusack, Wearn, et al., 2015;

Wells et al., 2004, 2006), potentially limiting foraging efficiency. Many species, such as tree shrews and squirrels, also exhibit limited dispersal capabilities that preclude them from re-colonizing fragmented islands from source populations in the mainland due to the inhospitable water matrix (Brunke et al., 2019; Henle et al., 2004), this disrupts the balance between the processes of extinction as populations decline within an environment and immigration which repopulates areas. These findings contrast with the high predictive power of the SAR found for small mammal communities isolated in reservoirs islands in the Amazon (Palmeirim et al., 2018), as well as for many other biological groups similarly isolated (Palmeirim et al., 2022).

In my study landscapes, island area indirectly explained small mammal richness declines as a highly dominant generalist species increased as islands got smaller, likely due to their high capability of surviving the harsher conditions posed by smaller islands compared with larger islands (Loveridge et al., 2016; Riofrío-Lazo & Páez-Rosas, 2015). The establishment of a *Rattus* population on an island is likely to cause additional pressure on native small mammal species through interference (Amarasekare, 2002), exploitation and/or apparent competition (Harper & Bunbury, 2015).

As insular fragmented landscapes become increasingly degraded, the resident small mammal community not only experiences both direct and indirect effects, but other taxa may also be impacted by some form of "ecological meltdown" (Terborgh et al., 2001), including large-bodied mammals (Dirzo et al., 2014), birds (Betts et al., 2022) and insects (Wagner et al., 2021). This can lead to trophic cascades within the ecosystem and the loss of important ecological functions (Dobson et al., 2006; Valiente-Banuet et al., 2015) with impaired seed dispersal of large-seeded species (Fontúrbel et al., 2015) further degrading the habitat, reduced carbon storage (Brinck et al., 2017), decreased pollination (Potts et al., 2010) and disrupted nutrient cycling (Haddad et al., 2015).

My results point to a shift from traditional island biogeographic and SAR models (Lomolino, 2000a; MacArthur & Wilson, 1963, 1967), showing that landscape degradation is an important factor affecting species richness in habitat isolates. Most research on the species-area relationship shows a 'relaxation' period (Diamond, 1972) as species gradually undergo local extinctions following the initial isolation event (Jones et al., 2016). However, my work shows that the complete collapse in the SAR is largely explained by habitat degradation and the proliferation of a generalist species, adding to a growing body of evidence on how habitat degradation modulates SARs (Öckinger & Smith, 2006; Schrader et al., 2019; Silva et al., 2022; Triantis et al., 2003). Habitat degradation not only directly leads to a suboptimal environment for primary forest species, but also facilitates the establishment and subsequent dominance of *Rattus*, further indirectly depressing small mammal richness. Further work is required to understand how species-area functions applied to other taxa are impacted by the degradation of habitat remnants. However, given my findings showing the wholesale upheaval of an ecologically important taxon, conservation efforts should focus on preserving large tracts of undisturbed habitat to retain maximum ecosystem functioning in the remaining tropical forest landscapes (Nakagawa et al., 2006; Stokes et al., 2009), as habitat that is heavily disturbed will be unable to sustain high levels of species diversity regardless of the size.

Chapter 4 : Detrimental effects of human-induced habitat degradation on vertebrate species-area relationships in insular paleotropical forest landscapes

Abstract

The equilibrium theory of island biogeography (ETIB), first proposed in the 1960s, is a virtually ironclad framework that has since shaped the direction of fragmentation ecology. However, a growing body of research has begun exploring the limitations of the ETIB framework in explaining community structure following fragmentation, by including additional modulating variables that could better explain species responses. Here, I assess the importance of habitat degradation in improving upon the ETIB model, using three archipelagic forest landscapes in Southeast Asia across a marked gradient of disturbance created by human activities such as cattle grazing and fires. For islands in all three landscapes were created by hydropower reservoirs and had been isolated over similar time periods. Using camera traps, I surveyed terrestrial vertebrates on island fragments and within the surrounding mainland continuous forest. I then examined if a model containing the traditional ETIB predictor variables — island size and isolation — performed better than alternative models including habitat degradation as represented by the Normalized Difference Vegetation Index (NDVI). Across landscapes, the model containing forest patch area with an interaction term with habitat degradation (ΔAICc = 0.0) outperformed the traditional ETIB model (ΔAICc = 14.5). At the landscape level, the explanatory power of forest patch area decreased as habitat degradation increased (Kenyir: $R^2 = 0.76$, $p < 0.001$; Chiew Larn: $R^2 = 0.54$, $p < 0.001$; Vajiralongkorn: $R^2 = 0.13$, $p = 0.187$), culminating in the complete collapse of the species area relationship (SAR). Habitat degradation was an important predictor of terrestrial vertebrate responses to forest fragmentation within land bridge island systems, indicating the limitations of the naïve ETIB framework in working human-modified landscapes. I also show how additional anthropogenic habitat degradation can substantially reduce the conservation value of forest remnants within modern hydropower reservoirs.

Introduction

Habitat loss and fragmentation typically results from land use change induced by human activities, profoundly altering terrestrial ecosystems (Haddad et al., 2015; Pereira et al., 2010; Rands et al., 2010), impacting reptiles (Keinath et al., 2017), birds (Bregman et al., 2014) and mammals (Kuipers et al., 2021). Forest fragmentation is occurring at an alarming rate. For instance, the proportion of forest edge area relative to total forest area in tropical regions has increased from 27% in 2000 to 31% in 2010 (Ma et al., 2023), with over 70% of all tropical, temperate and boreal forests now within 1 km of a hard edge (Haddad et al., 2015).

The species-area relationship (SAR) between remaining habitat area and species richness (Preston, 1962; P. Williams, 1964), which was first suggested in the 19th century (De Candolle, 1855; Watson, 1859), is a fundamental pattern in nature that has been extensively documented in the scientific literature (Lomolino, 2000a; Rosenzweig, 1995). Subsequently, the Equilibrium Theory of Island Biogeography (ETIB) framework (MacArthur & Wilson, 1963, 1967) was developed, expanding on the SAR pattern but including isolation distance to better predict the number of species on islands. ETIB has played a pivotal role over the past five decades in explaining species dynamics in insular fragmented landscapes and has shaped the field of fragmentation ecology (Warren et al., 2015). Despite the predictive utility of this framework, other variables might also be important in explaining patterns of species persistence in insular fragmented landscapes (Lomolino, 2000b), such as habitat quality, matrix quality, hunting pressure, and interactions with invasive species, all of which have been neglected by previous notions of island biogeography. In the face of accelerating anthropogenic disturbances, such as rapid urbanization, climate change, and habitat degradation, the simplistic equilibrium assumptions of ETIB may fail to capture the nature of species responses to habitat isolates embedded within an inhospitable matrix (Laurance, 2008; Lomolino, 2000b; Neto et al., 2022; Triantis et al., 2012).

Including measures of habitat quality within the traditional framework of ETIB has the potential to improve our understanding of how ecological communities drift in response to fragmentation, given the large body of research demonstrating the negative impacts of habitat degradation on ecological communities (Banks-Leite et al., 2020; Heinrichs et al., 2016). Newly fragmented forest landscapes are subjected to gradual or punctuated degradation due to several factors. For example, edge effects often induce changes in microclimatic conditions, often resulting in drier and warmer environments (Benchimol & Peres, 2015a; Laurance, 2008; Murcia, 1995). These altered environmental conditions can lead to an increase in windfalls, further opening up the forest canopy and causing additional collateral damage (Laurance & Curran, 2008). Consequently, this gradual shift in forest structure contributes to a change in the species composition of the forest ecosystem, often favouring pioneer species and transitioning towards an earlier successional system (Liu, Coomes, et al., 2019; Tabarelli et al., 2008).

In addition, this gradual decline in habitat quality can be substantially accelerated and intensified by human activities such as wildfires, which damages the understorey structure and prevents forest regeneration (Barlow et al., 2016; Bowman et al., 2009; Prestes et al., 2020). This eventually leads to a forest 'secondarization' process, often characterized by a nearly complete stand replacement following two to three recurrent fires (Barlow & Peres, 2008). Intensive cattle grazing and trampling can also accelerate habitat degradation by compacting the soil (Barzan et al., 2021; Landsberg et al., 2003) and thinning the understorey through seedling and sapling herbivory, which further disrupts forest regeneration. Considering the substantial alterations in plant communities in 'working landscapes' induced by both natural and anthropogenic processes, it is important to understand the degree to which other variables, such as natural or human-induced habitat disturbance, can improve the predictions of ETIB.

The combination of climatic alterations and functional homogenization of plant communities has substantial implications for terrestrial vertebrates, especially forest specialists, leading to extensive declines and local extinctions (Filgueiras et al., 2021; Tabarelli et al., 2012). Many specialist species have evolved to thrive in very specific old-growth forest niches but are now ill-equipped to deal with rapidly changing habitats due to their traits. For example, low-fecundity, dietary and habitat specialists that experience high metabolic requirements and exhibit limited dispersal capabilities are often penalized within small, degraded forest patches (Devictor et al., 2008; Henle et al., 2004; Pandit et al., 2009). In contrast, species bearing more generalist traits, such as a broad dietary breadth, fast reproduction, and a tolerance to anthropogenic environments, are more likely to persist within degraded landscapes (Chichorro et al., 2019; Franzén et al., 2012; Keinath et al., 2017).

To examine the often neglected role of habitat degradation in the persistence of biological communities stranded in forest fragments, I surveyed vertebrate assemblages across three insular fragmented tropical forest landscapes, created by the flooding of hydropower reservoirs. Although isolated for similar time periods, these archipelagic landscapes are characterized by different degrees of post-isolation habitat degradation, resulting from human-mediated degradation processes.

I hypothesised that, across the three landscapes, vertebrate species richness would be positively affected by forest area and negatively affected by forest isolation and forest degradation. However, these drivers of species richness may also change at the individual landscape level as the amount of habitat degradation increases, with habitat degradation becoming increasingly important in predicting species richness. As such, for the scenario of low habitat degradation, I expected the ETIB model to best explain patterns of terrestrial vertebrate species richness. For the intermediate habitat degradation scenario, I expected a decline in the predictive power of ETIB. Finally, for the high degradation scenario, I expected a nearly complete breakdown in the ability of the ETIB to explain terrestrial vertebrate richness patterns. I further expand on the advantages of incorporating habitat degradation to enhance the predictive power of ETIB models in tropical biotas.

Methods

Study sites

This study was undertaken in Southeast Asia (Figure 4.1A). Sampling was conducted within and around three hydropower reservoirs which caused the flooding of forest habitat, isolating hundreds of island fragments: Lake Kenyir in Terengganu, Peninsular Malaysia (geographic coordinates: 4.98, 102.64), Chiew Larn reservoir in Surat Thani, Thailand (9.12, 98.62) and Vajiralongkorn Dam in Kanchanaburi, Thailand (15.01, 98.53) (Figure 4.1B-D).

All three study landscapes were chosen for their different degrees in habitat disturbance while sharing similar landscape characteristics such as the large number of islands (100-400 per landscape), wide range in island size (0.6 – 1,428 ha), a common driver of insularization, long relaxation time (since 1984 for Vajiralongkorn and 1986 for Kenyir and Chiew Larn) and a considerable overlap in species composition (57% of all mammal species are found in all three landscapes and 85% are found in at least two landscapes). Importantly, however, these three landscapes span a gradient of anthropogenic disturbance, allowing for the comparison of faunal change relative to landscape degradation. Although all landscapes had experienced selective timber extraction during the creation of their dams, Kenyir remains the least degraded landscape with a relatively intact canopy and understorey; Chiew Larn has experienced declines in structural complexity of the understorey shifting towards increasing dominance of pioneer species; and Vajiralongkorn is considerably degraded with the addition of human-mediated disturbances such as fires and livestock grazing.

As a proxy, this disturbance was represented by the Normalized Difference Vegetation Index (NDVI) (Figure 4.1E). NDVI is one of the most widely used spectral indices in remote sensing, identifying vegetation areas and their characteristics (Pettorelli et al., 2005), and has been repeatedly used to understand the impacts of land use change and degradation on animal communities (Elbahi et al., 2023; Holm, 2003; Thiam, 2003; Tovar, 2012; Vogelmann et al., 2017).

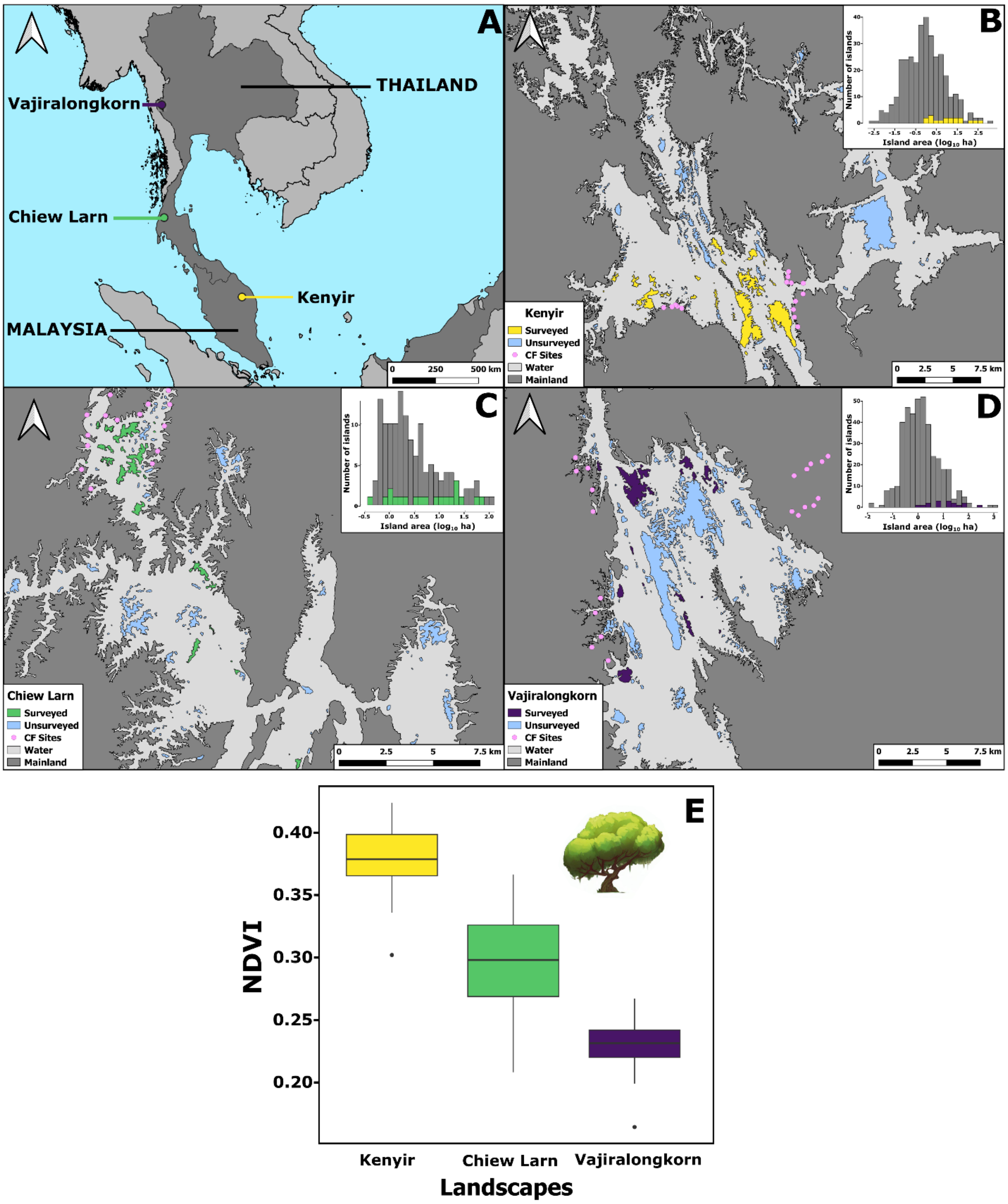


Figure 4.1. A map of part of Southeast Asia showing the locations of all three landscapes examined in this study: (A), Kenyir (B), Chiew Larn (C), Vajiralongkorn (D). Distribution of island sizes contained within each reservoir. All surveyed sites are coloured; unsurveyed islands are shown in blue. NDVI for surveyed islands within each landscape are represented in a boxplot (E), in which solid dots indicate outliers.

Landscape description

The insular fragmented landscape at Kenyir is the largest man-made lake in mainland Southeast Asia, comprised of >340 islands with sizes spanning 0.6 ha to 1,428 ha. The reservoir was formed in 1986 for the construction of the Kenyir Dam, inundating over 2,600 km^2 of lowland and mid-elevation dipterocarp forest. The climate of the region consists of a marked dry season spanning May to October and a wet season from November to April, with an annual rainfall of 2,700 mm to 4,000 mm (Qie et al., 2011). Taman Negara National Park borders the southeast of the reservoir in which the control continuous forest plots were placed.

The insular fragmented landscape at Chiew Larn is comprised of >100 islands ranging from <1 ha to >100 ha in area. The reservoir was formed in 1986 due to the construction of Rajjaprabha Dam, inundating 165 km^2 of lowland monsoon evergreen forest. The climate of the region has an average annual temperature of 26.8°C and rainfall averaging 2,365 mm. The landscape falls under the protection of two areas, Khao Sok National Park established in 1980, spanning 739 km^2, and Khlong Saeng Wildlife Sanctuary established in 1974, spanning 1,115 km^2 in which the control contiguous forest sites are situated.

The insular fragmented landscape at Vajiralongkorn is comprised of >400 islands ranging from <1 ha to >900 ha. The reservoir was formed in 1984 due to the construction of Vajiralongkorn Dam, inundating 1,497 km^2 of mixed deciduous and hill evergreen forest. The climate of the region consists of three distinct seasons, a hot season spanning February to May, a rainy season spanning June to October, and a cold season spanning November to January. The reservoir is bordered to the east by Khao Laem National Park covering 1,497 km^2, in which the control contiguous forest camera traps reside.

Vertebrate surveys

Vertebrate assemblages were surveyed using camera-trapping, which allowed me to record not only mammals but also some large-bodied birds and reptiles. The number of camera traps allocated per island was proportional to island area (Schoereder et al., 2004); specifically, islands smaller than 20 ha were assigned one camera trap, islands ranging from 20 to 50 ha were allocated two camera traps, and islands larger than 50 ha were surveyed using three camera traps. In addition to surveyed islands, three continuous forest (CF) locations were also surveyed as pseudo-control sites at all three landscapes. Each CF site was surveyed using five camera traps, all of which were located at least 500 m away from the reservoir edge. At each camera trap site, I deployed a single Bushnell camera trap, at a standard height of 50 cm from ground level, attached to trees facing an intersecting animal trail, although I acknowledge trail bias may occur potentially affecting detectability of some species (Cusack, Dickman, et al., 2015; Kolowski & Forrester, 2017). Cameras were set on photo mode and had a 5-sec delay between consecutive triggers. No bait was used at the camera trap locations. The temporal independence threshold of consecutive photos defined as 'independent photos' of individuals of the same species at the same was 30 minutes.

At Kenyir, I surveyed a total of 28 islands, deploying 44 cameras for a total of 1,493 trap-nights, averaging 34 nights per camera. This culminated in 47,029 photos, which after processing resulted in 1,966 independent species photo detections. At Chiew Larn, I surveyed a total of 20 islands, deploying 27 cameras for a total of 1,205 trap-nights, averaging 45 nights per camera. This culminated in 28,592 photos, which after processing resulted in 1,159 independent species photos. At Vajiralongkorn, I surveyed a total of 15 islands, deploying 24 cameras for a total of 1,118 trap-nights, averaging 47 nights per camera. This culminated in 93,169 photos, which after processing resulted in 542 independent species photos.

Environmental variables

All environmental variables were generated and extracted using the QGIS program (QGIS.org, 2023). Two patch- and landscape variables were generated to represent island size and isolation: forest patch area ($\log_{10} x$) and distance to the mainland (m), as postulated by the ETIB. Distance to the nearest island was also generated as an alternative isolation metric using the distance matrix function in QGIS. Island sizes and distance to the mainland were extracted using open street map data (OSM, 2020). For mainland sites, forest patch area was arbitrarily assigned to one order of magnitude higher than the largest island at each archipelagic landscape, and distance to mainland was set to zero.

Landscape cover and percentage forest cover were generated to examine the habitat amount hypothesis modelling framework (Fahrig, 2013). The Global Forest Cover Change Tree Cover Multi-Year Global raster layer for 2015 (Townshend, 2016) was used to calculate landscape cover. Open water areas were masked and removed from the forest cover layer. A total of 40 buffer sizes were generated from 50-2000 m around all island centroid points and at all contiguous forest sites. Zonal statistics were then calculated for all buffer sizes, thereby resulting in forest cover estimates at 40 different scales. These scales were then tested to examine the strength of correlation values between island size and habitat amount to assess the suitability of the multiple linear regression test see (A. S. Bueno & Peres, 2019). I therefore calculated the "scale of effect" (Martin & Fahrig, 2012) i.e., the spatial scale at which the investigated response (i.e. species richness) is maximised, using the 'multifit' package and function (Huais, 2018). I identified that 350 m and 400 m were the most appropriate scales for islands and continuous forest sites, respectively, in explaining the variation in my response variables.

Two bands of Landsat 8, the land surface reflectance product (Vermote et al., 2016), were used to generate a new NDVI raster. I used the QGIS raster calculator to subtract the red band values from the near-infrared bands and divided the result by the sum of the red and near-infrared bands. I then performed zonal statistics on the new NDVI raster layer using vector shapes for surveyed islands, calculating the mean raster NDVI value for each island. NDVI for mainland sites was calculated using a 500 m buffer around the camera trap placement, the average distance between camera trap points. NDVI was calculated as the mean annual value, based on 12 months of Landsat 8 imagery from 2020, which was the year when the majority of the data was collected. This method was employed to minimize the variation in productivity or forest seasonality that might arise if Landsat 8 imagery from a single month was used to generate NDVI values.

Island shape index was also generated calculated as (Perimeter / (π × Area × 2)) representing the amount of edge habitat.

Data analysis

All camera trap data were standardised to 100 trap nights (rounded to whole number) per camera trap location and all analyses were performed within the R statistical program version 4.3.2 (R Core Team, 2023). To examine the best predictor variables for terrestrial vertebrate richness across all landscapes, a Generalised linear mixed model (GLMM) was applied, generated with the ‘lme4’ R package (Bates et al., 2015). The following environmental variables – forest patch area, isolation, distance to nearest island (m), NDVI and shape index – were included in a global model with an interaction term between forest patch area and NDVI. A random effect for landscape was included and a Poisson family structure was used. The dredge function, from the MuMIn package (Bartoń, 2009), was used to generate a full combination of models for which model selection filtered the best models with delta AICc values lower than 2 (ΔAICc<2.0) to create an averaged model.

To examine the ‘best’ predictor variables for terrestrial vertebrate species richness for each individual landscape, I fitted Generalized linear models (GLMs) using the same global model stated previously but without a random effect for landscape. Both models for Kenyir and Chiew Larn used Poisson families, but a negative binomial family was used for Vajiralongkorn. The dredge function was also used, and a model selection was completed.

The model with the lowest AICc was chosen as the best predicting model for the landscape.

Results

NDVI

Mean (± SD) forest canopy NDVI per insular landscape was 0.378 (± 0.038), 0.297 (± 0.038), and 0.230 (± 0.026), at Kenyir, Chiew Larn and Vajiralongkorn, respectively (Figure 4.1E). For mainland sites the mean NDVI was 0.298 (± 0.043), 0.326 (± 0.015) and 0.326 (± 0.042) at Kenyir, Chiew Larn and Vajiralongkorn, respectively. Welch two-samples t-tests showed that mean NDVI for surveyed islands was significantly different between all three study landscapes: Kenyir vs Chiew Larn (t = -7.23, df = 35.27, $p < 0.001$), Chiew Larn vs Vajiralongkorn (t = 6.19, df = 32.871, $p < 0.001$) and Kenyir vs Vajiralongkorn (t = 15.515, df = 31.93, $p < 0.001$).

Species richness

The total number of species detected per landscape was 35, 31 and 41 for Kenyir, Chiew Larn and Vajiralongkorn, respectively. On islands, the total (and mean ± SD) number of species on islands was 28 (4.56 ± 3.80), 21 (5.80 ± 3.02) and 19 (4.00 ± 1.93) in Kenyir, Chiew Larn and Vajiralongkorn, respectively. Within mainland sites the total (and average ± SD) number of species was 25 (6.38 ± 1.45), 27 (7.93 ± 1.58) and 30 (7.80 ± 2.70), in Kenyir, Chiew Larn and Vajiralongkorn, respectively. The mammal species richness on islands was lower as the degradation of the landscape increased, with 19, 16, and 13 species found in Kenyir, Chiew Larn and Vajiralongkorn, respectively. The richness of mammals in the mainland sites was also lower as degradation increased, with 22, 20 and 17 species in Kenyir, Chiew Larn and Vajiralongkorn, respectively. Bird species richness on islands was 8, 4 and 6 for Kenyir, Chiew Larn and Vajiralongkorn, respectively. In the mainland sites, bird richness was almost four times higher in the most degraded landscape compared with the most pristine landscape, with 3, 6 and 11 species found in Kenyir, Chiew Larn and Vajiralongkorn, respectively.

At the Kenyir landscape, the most frequently detected species on islands and within the mainland was Wild boar (*Sus scrofa*). Islands within Kenyir also presented high detection rates of Mouse deer (*Tragulus* spp) while the mainland presented more detections of Muntjac deer (*Muntiacus muntjak*). At the Chiew Larn landscape, a higher number of herbivorous species were detected, including Mouse deer, Sambar deer (*Rusa unicolor*), Malayan porcupine (*Hystrix brachyura*), Gaur (*Bos gaurus*) and Asian elephants (*Elephas maximus*), along with the omnivorous Wild boar. At the Vajiralongkorn landscape, birds were highly prominent with 6 species of birds detected on islands and 11 species detected within the mainland, with most detections represented by Red jungle fowl (*Gallus gallus*) and Cattle egret (*Bubulcus ibis*). Within islands, domestic cattle and water buffalo were the most detected species while many large-bodied wild herbivores were not detected, including Sambar deer, Gaur and Asian elephant. Within islands at all landscapes, detections of primates and carnivores were limited.

Drivers of species richness across landscapes

GLMM averaging showed that both island size (estimate = 0.502 ± 0.05, $z = 9.05$, $p < 0.001$, CI $_{min}$ = 0.393, CI $_{max}$ = 0.610) and the interaction between island size and NDVI (estimate = 0.096 ± 0.05, $z = 9.05$, $p < 0.002$, CI $_{min}$ = 0.065, CI $_{max}$ = 0.320) were significant predictors of vertebrate species richness using data across all landscapes (Figure 4.2; Table 4.1). The interaction term between forest patch area and NDVI provides a representation of the degree to which these two variables jointly influence species richness.

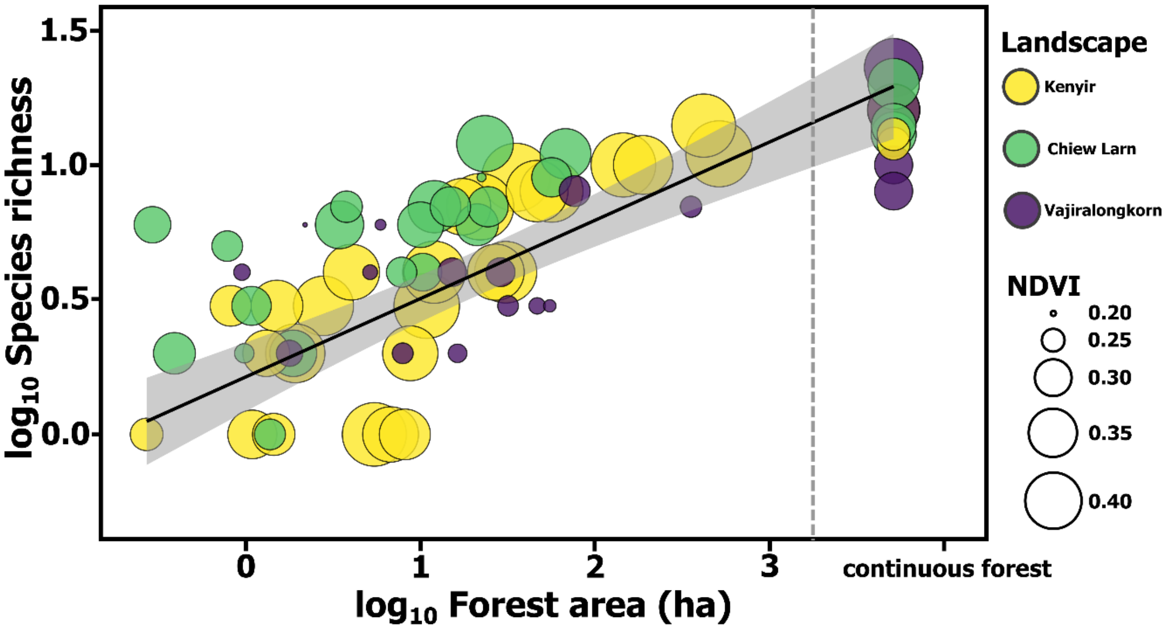


Figure 4.2. Vertebrate species richness for all three study landscapes in relation to island size. Circle sizes are proportional to NDVI values. The predicted linear fit is based on the GLMM model average with grey shading indicating 95% confidence interval regions. Circles are colour-coded according to landscape. Dashed grey line separates islands from continuous forest sites in the mainland of each landscape.

Table 4.1. GLMM model average output retaining only ΔAICc<2.0 models. Response variable estimated species richness. Landscape variables include forest patch area, distance to the mainland, distance to the nearest island, NDVI, shape index and an interaction term between forest patch area and NDVI. Statistically significant variables are indicated with an *.

Predictor variable	**Estimate**	**Std. Error**	**Adjusted SE**	**z value**	***p* value**	**CI $_{min}$**	**CI $_{max}$**
Forest patch area	0.501	0.054	0.055	9.047	< 0.001*	1.431	1.810
NDVI	0.096	0.069	0.070	1.375	0.169	0.393	0.610
Forest patch area x NDVI	0.193	0.063	0.065	2.97	0.002*	-0.041	0.234
Isolation	-0.122	0.086	0.087	1.4	0.161	0.065	0.320
Shape index	0.087	0.061	0.062	1.403	0.160	-0.294	0.049

Drivers of species richness at individual landscapes

Within the Kenyir landscape, the model containing forest patch area only (estimate = 0.669 ± 0.092, $z = 7.25$, $p < 0.001$, CI $_{min}$ = 0.490, CI $_{max}$ = 0.853) was the primary predictor of species richness, accounting for 76% of the variation in the data. At Chiew Larn, the model containing forest patch area only (estimate = 0.413 ± 0.105, $z = 3.95$, $p < 0.001$, CI $_{min}$ = 0.213, CI $_{max}$ = 0.623) best predicted species richness, accounting for 54% of variation. At Vajiralongkorn, the model containing forest patch area only (estimate = 0.244 ± 0.185, $z = 1.318$, $p = 0.187$, CI $_{min}$ = -0.121, CI $_{max}$ = 0.606) was the best predictor, but only accounted for only 13% of the variation in the data (Figure 4.3; Table 4.2).

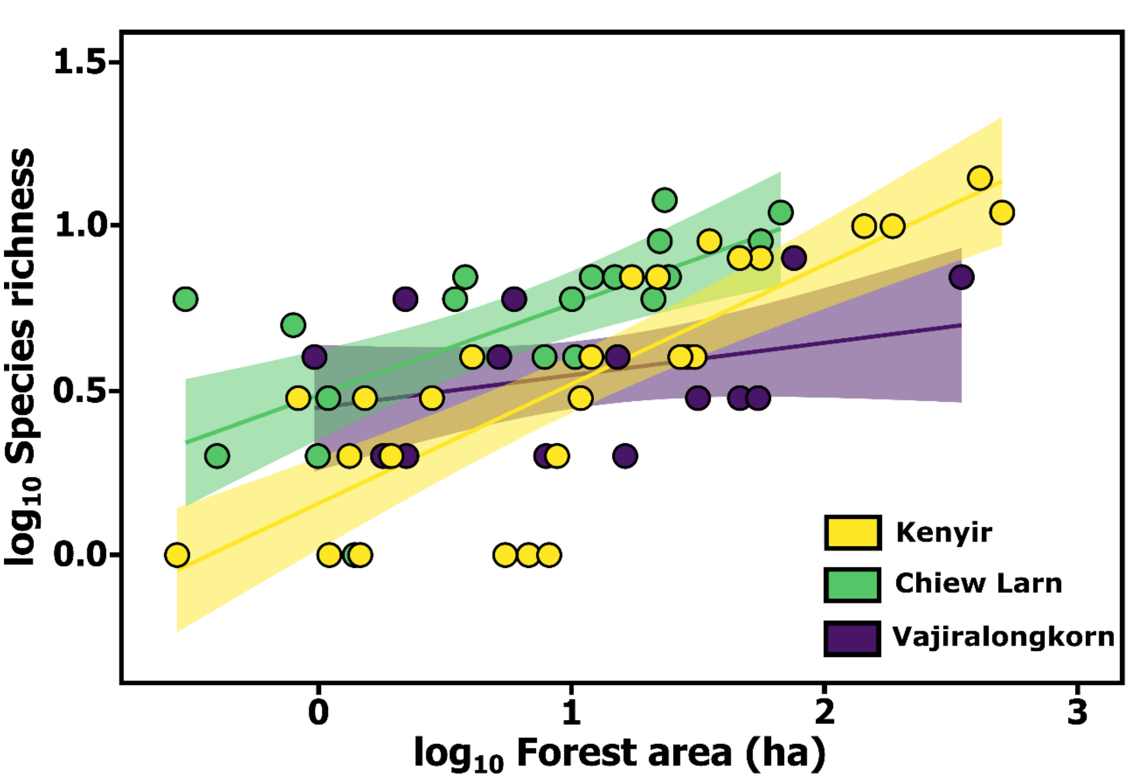


Figure 4.3. Relationship between vertebrate species richness and forest patch area (ha; $\log_{10} x$) for each of the study landscapes: Kenyir Lake (yellow), Chiew Larn (green), and Vajiralongkorn (purple). Solid lines represent the linear predictions from the corresponding GLM and shaded areas indicate 95% confidence intervals.

Table 4.2. Best GLM models explaining the variation in vertebrate species richness at the Kenyir (KY), Chiew Larn (CL), and Vajiralongkorn (VK) study landscapes. Tested landscape variables included forest patch area, distance to the mainland, distance to the nearest island, NDVI, and patch shape index; but only forest patch area presented explanatory power.

Landscape	**Predictor variables**	**Estimate**	**Std. Error**	**z value**	***p* value**	**R^2**	**CI $_{\text{min}}$**	**CI $_{\text{max}}$**
KY	Forest patch area	0.669	0.092	7.25	< 0.001	0.76	0.490	0.853
CL	Forest patch area	0.414	0.105	3.955	< 0.001	0.54	0.213	0.623
VK	Forest patch area	0.244	0.185	1.318	0.187	0.13	-0.121	0.606

Discussion

Using a dataset of terrestrial mammals and birds surveyed within three Southeast Asian archipelagic landscapes of increasing habitat degradation, I document the complete collapse of the species-area relationship — a fundamental pattern in ecology (Lomolino, 2000a; Rosenzweig, 1995) — within the most degraded landscape. I also show the importance of including forest habitat degradation as a modulating variable to improve the explanatory power of the ETIB model framework. Using data across all landscapes, the model containing forest patch area with an interaction term for forest habitat degradation (ΔAICc = 0.0) outperformed the traditional ETIB model (ΔAICc = 14.5). In other words, species richness increased on larger islands but was reduced by habitat degradation. These results add to a growing body of literature demonstrating the limitations of the unqualified ETIB framework by considering co-occurring environmental stressors that also affect community structure, such as habitat quality, matrix quality, strength of edge effects, degree of hunting pressure, and invasive species (Benchimol & Peres, 2013; Koh & Ghazoul, 2010; Matthews et al., 2016; J. H. Moore et al., 2022; Triantis et al., 2012). By identifying and exploring factors beyond the traditional ETIB framework, this study enhances our understanding of the intricate dynamics governing species retention in habitat isolates.

Habitat quality is an extremely important variable as it has the potential to impact species richness in a multitude of ways, collectively shaping the ecological dynamics of an environment. Edge effects for example, are a well-studied phenomenon, occurring at the interfaces between the forest and the surrounding matrix, disrupting ecological processes and creating transitional zones where certain species may struggle to adapt, thereby contributing to a reduction in overall species richness (Murcia, 1995). When a forest experiences a fragmentation event through human modification, it introduces edges within the forest matrix. Edge-dominated habitats affect microclimatic conditions producing drier and hotter environments (Gardner et al., 2018), and increasing susceptibility to wind falls, which may further exacerbate edge effects (Laurance 2008; Benchimol & Peres 2015b). These effects are often detrimental to long-lived canopy trees, leading to an ecosystem with a simplified structure dominated by generalist plant species (Liu, Coomes, et al., 2019; Tabarelli et al., 2008, 2012). One such pioneer species is bamboo, which was present at all sites but became increasingly prevalent as landscape degradation increased. This was the case of the islands at Vajiralongkorn, where bamboo completely dominated the landscape and further reduced the understorey complexity, contributing to the homogenization of animal communities.

However, the gradual impacts of edge effects alone do not entirely explain the gradient of habitat disturbance between the three study landscapes, which have been isolated for similar periods of time. At Chiew Larn, it is possible that native herbivores have negatively affected forest regeneration on islands through understorey overgrazing (Ramirez et al., 2019, 2021), with a large range of herbivorous species detected on the islands. Partially disturbed forests are more productive and contain more palatable plant species, attracting herbivores especially in the absence of predators (Reiner et al., 2023). Higher abundance of herbivores within an ecosystem have been documented to substantially impact the regeneration capability of natural forests, leading to open areas and reduced understorey complexity, which can compound edge effects (Maron & Crone, 2006; Ramirez et al., 2019; Xu et al., 2023). The islands in Chiew Larn are also dominated by hyperabundant rodents (J. H. Moore et al., 2022), which potentially limit forest recovery over time through elevated seed predation (Lopez & Terborgh, 2007). These hyperabundant rodents also reduce the diversity of native rodents (J. H. Moore et al., 2022), which may previously have served as important seed dispersal agents (Brewer & Rejmánek, 1999; Godó et al., 2022).

The insular fragmented landscape at Vajiralongkorn is considerably more degraded than Chiew Larn, likely due to the heavy presence of domestic bovine cattle on islands. Cattle strip all of the understorey vegetation, moving from island to island, opening up bare ground, destroying saplings, and exacerbating habitat degradation (Barzan et al., 2021; Landsberg et al., 2003) (Figure 4.4). In addition, human mediated fires occur across the landscape, further damaging the forest structure and preventing regeneration (Bowman et al., 2009; Prestes et al., 2020). The combination of cattle, human induced fires and accelerated edge effects likely substantially degraded the forest at Vajiralongkorn leading to a decline in the native vertebrate fauna.

Figure 4.4. High densities of domestic cattle grazing on an island within the Vajiralongkorn landscape.

Habitat quality often drives mammal use of space and habitat use (Regolin et al., 2021), while other studies have shown lizard responses to habitat quality (Silva et al., 2022). A global analysis of species traits also shows how habitat specialists and carnivores are particularly vulnerable to fragmentation effects (Keinath et al., 2017). This is because habitat specialists are often poorly adapted to landscape changes, often exhibiting narrow dietary breadths with specific resource requirements (Henle et al., 2004). Species likely to persist in highly degraded landscapes are those that possess generalist traits, such as high dispersal capacity, opportunistic foraging and high behavioural tolerance to human activity (Devictor et al., 2008; Filgueiras et al., 2021; Gibson et al., 2011). This is an ecosystem-wide issue affecting not only mammals (Dirzo et al., 2014) but also birds (Betts et al., 2017), insects (Wagner et al., 2021), and other taxa.

Reduced species richness has the potential to initiate a cascade of detrimental consequences that extend across several ecological functions, with repercussions for the overall health and stability of ecosystems (Dobson et al., 2006; Valiente-Banuet et al., 2015). Examples of functional disruption include declines in zoochoric seed dispersal, particularly of large-seeded plant species, subsequently preventing effective regeneration of plant communities (Estes et al., 2011; Fontúrbel et al., 2015; Lindsell et al., 2015; Ripple et al., 2015). Disrupted nutrient cycling, particularly in the presence of large domestic herbivores which strip nutrients from the ecosystem (Haddad et al., 2015;

Nichols et al., 2009; Proesmans et al., 2022), lead to declines in forest structure through direct trampling and overgrazing (Li & Jiang, 2021), which may reduce carbon storage (Brinck et al., 2017). Weakened stability and resilience of the ecosystem can also occur as the balance between species is eroded (Oliver et al., 2015). For example, this may lead to lower resistance to the invasion by non-native species as high native species richness helps to maintain the integrity of native ecosystems (Eschtruth & Battles, 2009; Mungi et al., 2021). In extreme cases, this can ultimately lead to wholesale shifts in the structure of the ecosystem and a complete 'ecological meltdown' (Terborgh et al., 2001).

Limitations

The findings of this study are promising in demonstrating some potential limitations to the ETIB framework. However, I acknowledge that NDVI is only a crude proxy for habitat degradation (Tovar, 2012), providing information on photosynthetic productivity and on the forest canopy density, but was the highest quality data available to represent the canopy topology of the study landscapes. More accurate metrics to represent habitat degradation could include vegetation surveys to more accurately measure understorey vegetation structure and changes in plant species composition (DeWalt et al., 2003), drone or ground based LiDAR scanning to measure canopy height and fracture (Bradbury et al., 2005), and direct measurements of sunlight, humidity and temperature. This study also only focuses on species richness as a coarse metric of community structure; additional metrics based on abundance-weighed community composition and functional diversity (Chao et al., 2014) would further elaborate on the impacts of habitat degradation on species communities.

Conclusion

Understanding and considering additional predictor variables is crucial to accurately predict and mitigate species declines in the face of human-induced landscape degradation. Island biogeography theory has been extremely influential in shaping five decades of conservation planning worldwide (Currie, 2010; Matthews & Triantis, 2021) but its naïve framework remains limited in explaining species responses to insular fragmentated landscapes experiencing high levels of human-mediated habitat degradation. Human landscape degradation not only contributes to immediate species declines but also elevates the rate and extent to which extinction debts are paid (Diamond, 1972; Jones et al., 2016). With modern ecological tools and metrics, more complex models can now more accurately inform conservation policies. Moreover, it is evident that the conservation value of relict islands in hydropower reservoirs becomes even more precarious in the presence of heightened degradation. As these fragments are already susceptible to isolation effects, escalating degradation compounds their vulnerability. It is clear that the establishment of hydropower dams have major widespread impacts on the resident animal communities and provide limited conservation value, especially when additional human-mediated degradation occurs. Future research focusing on functional traits can provide insights into the adaptive capacities of species and inform conservation efforts aimed at preserving not only species richness but also the ecological functions and resilience of ecosystems in the face of ongoing anthropogenic pressures.

Chapter 5 : The rise of hyperabundant native generalists threatens humans and conservation

Abstract

In many disturbed terrestrial landscapes, a subset of native generalist vertebrates thrives. The population trends of these disturbance-tolerant species may be driven by multiple factors, including habitat preferences, foraging opportunities (including crop raiding or human refuse), lower mortality when their predators are persecuted (the 'human shield' effect) and reduced competition due to declines of disturbance-sensitive species. A pronounced elevation in the abundance of disturbance-tolerant wildlife can drive numerous cascading impacts on food webs, biodiversity, vegetation structure and people in coupled human–natural systems. There is also concern for increased risk of zoonotic disease transfer to humans and animals from species with high pathogen loads as their abundance and proximity to humans increases. Here I use field data from 58 landscapes to document a supra-regional phenomenon of the hyperabundance and community dominance of Southeast Asian wild pigs and macaques – two mammalian groups which often accounted for >50% of all detections from camera trap studies. These groups were chosen as prime candidates capable of reaching hyperabundance as they are edge adapted, with omnivorous diets, rapid reproduction and high tolerance to human proximity. Compared to intact interior forests, population densities in degraded forests were 148% and 87% higher for wild boar and macaques, respectively. In landscapes with >60% oil palm coverage, wild boar and pig-tailed macaque estimated abundances were 337% and 447% higher than landscapes with <1% oil palm coverage, respectively, suggesting marked demographic benefits accrued by crop raiding on calorie-rich food subsidies. There was extreme community dominance in forest landscapes with >20% oil palm cover where two pig and two macaque species accounted for >80% of independent camera trap detections, leaving only 20% for the other 85 mammal species >1 kg considered. Establishing the population trends of pigs and macaques is imperative since they are linked to cascading impacts on the fauna and flora of local forest ecosystems, and human health and economics. The severity of potential negative cascading effects may motivate control efforts to achieve ecosystem integrity, human health and conservation objectives. My review concludes that the rise of native generalists can be mediated by specific types of degradation, which influences the ecology and conservation of natural areas, creating both positive and detrimental impacts on intact ecosystems and human society.

Introduction

Disturbance-tolerant wildlife

There are numerous reasons why native wildlife thrives near humans and human-modified landscapes, including favourable habitat features, foraging opportunities or reduced predation and competition (Filgueiras et al., 2021; Gaynor et al., 2019). Native terrestrial mammals are sustained in a variety of human–natural systems, where they are part of food webs, contribute to ecosystem processes and in turn provide humans with ecosystem services (Apfelbeck et al., 2020; Collins et al., 2021). These positive impacts are balanced by deleterious effects if wildlife poses risks to humans and livestock, such as direct attacks, *via* zoonotic diseases, or damage to crops or other products (Gibb et al., 2020; Luskin, Brashares, et al., 2017; Luskin, Meijaard, et al., 2021). Human tolerance of wildlife also depends on conservation threat levels. For example, Critically Endangered pangolins (*Manis javanica*) are tolerated in Singapore despite elevated zoonotic disease risks (IUCN, 2019; Nursamsi et al., 2023), while Least Concern civets and bats hosting viral pathogens, including Nipah, SARS and likely COVID-19, may not be tolerated (Dehaudt et al., 2022; Dunn et al., 2022; Gibb et al., 2020; Yu et al., 2018). The densities of human commensal wildlife also shape attitudes towards the species and the magnitude of their positive or negative impacts.

Wildlife in degraded habitats

Over 70% of the world's remaining forests are within 1 km of an edge (Haddad et al., 2015). The increasing proportion of edge habitat negatively affects forest specialists and increases access for hunters, who preferentially target large-bodied vertebrates (Benítez-López et al., 2017; Peres, 2001). While many species respond negatively to forest edges, a subset of generalist species can thrive in these degraded areas, particularly those species that can exploit disturbed and human-modified habitats and resources (Gibson, 2011; Luskin, Brashares, et al., 2017). These 'winners' can even reach hyperabundance, greatly exceeding natural densities supported by undisturbed habitats and consequently produce negative impacts on other native fauna and flora (Filgueiras et al., 2021).

Wildlife hyperabundance

Definition

I define hyperabundance in native mammals as at least a doubling of their long-term population density, compared with similar habitats, that is driven by non-natural, human-caused conditions. This definition takes into account the known variation in densities within species that span multiple ecosystems (e.g. grasslands *versus* deciduous forests) or when they are closely tied to predator–prey dynamics (Berryman, 1992). Species like rodents with *r*-selected life histories (prolific reproduction, high mortality, short-lived) may appear predisposed to hyperabundance since they can double their populations within a single year (Fryxell et al., 2014), but I reserve the term hyperabundance for situations with persistently elevated densities across multiple years (e.g. Gibson *et al.*, 2013; Moore *et al.*, 2022).

Drivers of hyperabundance

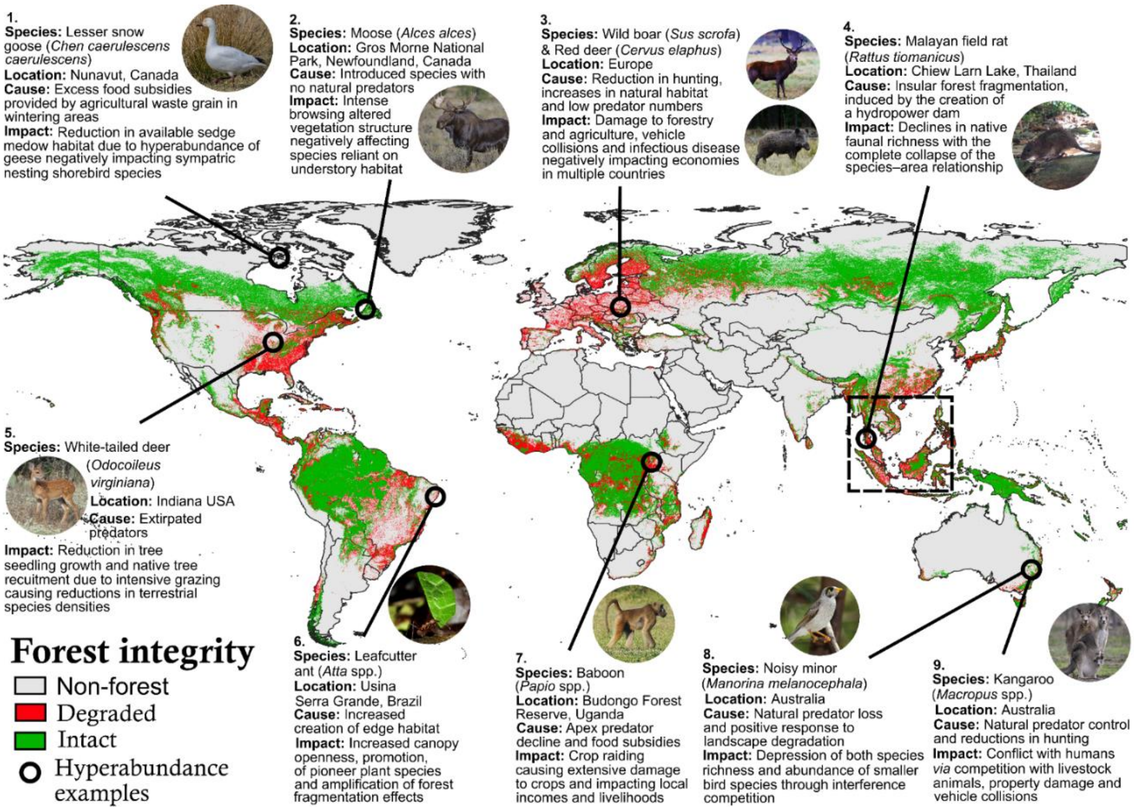
Wildlife hyperabundance in degraded landscapes can arise through several processes. Species traits associated with hyperabundance may include being habitat and dietary generalists that naturally thrive in ecotones and edges, or species with high fecundity whose populations can respond to changing resources or withstand hunting pressure (Filgueiras et al., 2021; Terborgh & Estes, 2013). Hyperabundance is also found in species that leave natural areas to exploit anthropogenic food subsidies (i.e. crop raiding) and in species considered unpalatable due to food taboos or that are uninteresting for the pet and medicine trade (Luskin et al., 2014; Luskin, Brashares, et al., 2017; Oro et al., 2013).

Hyperabundance globally

Examples of hyperabundance can be found in a variety of species and ecosystems, indicating this is a global phenomenon (Figure 5.1). Hyperabundant native generalists are often associated with humans and cause severe ecological damage (Estes et al., 2011; Luskin, Brashares, et al., 2017) and alter plant and animal diversity (Dirzo et al., 2014; Estes et al., 2011; Ivey et al., 2019; Terborgh & Estes, 2013). Hyperabundant species may also be associated with human–wildlife conflict such as crop raiding (Luskin et al., 2014; Taylor et al., 2016), property damage (Barrios-Garcia & Ballari, 2012), and outbreaks of zoonotic diseases such as rabies and Lyme disease (Gibb et al., 2020; Levi et al., 2012). There is an especially urgent need for a large-scale synthesis to understand the patterns, drivers, and consequences of hyperabundant generalist species in regions suffering high rates of biodiversity loss, habitat degradation, and histories of zoonotic disease emergence, all of which may be aggravated by high human population densities.

Hyperabundance in Southeast Asia

Hyperabundance in Southeast Asia is poorly understood (Amir, Moore, et al., 2022). To date, clear results have only been reported for Malayan field rats (*Rattus tiomanicus*) on man-made islands (J. H. Moore et al., 2022), wild boar (*Sus scrofa*) in one forest in Peninsular Malaysia (Ickes, 2001; Luskin, Brashares, et al., 2017), and sporadic reports suggesting high densities of long-tailed macaques (*Macaca fascicularis*) that require management in Peninsular Malaysia (Choong et al., 2021). There are no clear regional trends for pigs and macaques and these taxa are actually presumed to be declining in most accounts (M. F. Hansen et al., 2023; Ke & Luskin, 2019; Keuling & Leus, 2019; Luskin et al., 2018; Luskin, Meijaard, et al., 2021; Luskin, Moore, et al., 2023; Luskin & Ke, 2017; Ruppert et al., 2022). In Southeast Asia, there are reports of wild boars and bearded pigs *Sus barbatus* benefiting from oil palm but these all arose from single-landscape studies. Studies at Pasoh Forest Reserve in Peninsular Malaysia (Ickes et al., 2001; Luskin, Brashares, et al., 2017), Sumatra (Luskin et al., 2014), and Sabah, Borneo (Love et al., 2017) have shown positive responses of wild boars and bearded pigs to oil palm. There is equally as much work suggesting wild boars and bearded pigs are declining in the region (Harrison et al., 2016; Luskin et al., 2018) with the lethal onslaught of African Swine Fever threatening extirpations and extinctions (Luskin, Meijaard, et al., 2021; Luskin, Moore, et al., 2023). For macaques, recent work suggested that pig-tailed macaques *Macaca nemestrina* are increasingly threatened, leading to the IUCN *Red List* upgrading their threat status from Vulnerable to Endangered, i.e. the opposite of hyperabundance (Ruppert et al., 2022).



1.
Species: Lesser snow goose (*Chen caerulescens caerulescens*)
Location: Nunavut, Canada
Cause: Excess food subsidies provided by agricultural waste grain in wintering areas
Impact: Reduction in available sedge medow habitat due to hyperabundance of geese negatively impacting sympatric nesting shorebird species

2.
Species: Moose (*Alces alces*)
Location: Gros Morne National Park, Newfoundland, Canada
Cause: Introduced species with no natural predators
Impact: Intense browsing altered vegetation structure negatively affecting species reliant on understory habitat

3.
Species: Wild boar (*Sus scrofa*) & Red deer (*Cervus elaphus*)
Location: Europe
Cause: Reduction in hunting, increases in natural habitat and low predator numbers
Impact: Damage to forestry and agriculture, vehicle collisions and infectious disease negatively impacting economies in multiple countries

4.
Species: Malayan field rat (*Rattus tiomanicus*)
Location: Chiew Larn Lake, Thailand
Cause: Insular forest fragmentation, induced by the creation of a hydropower dam
Impact: Declines in native faunal richness with the complete collapse of the species–area relationship

5.
Species: White-tailed deer (*Odocoileus virginiana*)
Location: Indiana USA
Cause: Extirpated predators
Impact: Reduction in tree seedling growth and native tree recuitment due to intensive grazing causing reductions in terrestrial species densities

6.
Species: Leafcutter ant (*Atta* spp.)
Location: Usina Serra Grande, Brazil
Cause: Increased creation of edge habitat
Impact: Increased canopy openness, promotion, of pioneer plant species and amplification of forest fragmentation effects

7.
Species: Baboon (*Papio* spp.)
Location: Budongo Forest Reserve, Uganda
Cause: Apex predator decline and food subsidies
Impact: Crop raiding causing extensive damage to crops and impacting local incomes and livelihoods

8.
Species: Noisy minor (*Manorina melanocephala*)
Location: Australia
Cause: Natural predator loss and positive response to landscape degradation
Impact: Depression of both species richness and abundance of smaller bird species through interference competition

9.
Species: Kangaroo (*Macropus* spp.)
Location: Australia
Cause: Natural predator control and reductions in hunting
Impact: Conflict with humans *via* competition with livestock animals, property damage and vehicle collisions

Figure 5.1. Examples of hyperabundant native wildlife with the dashed square indicating my study area. Colours on the map represent the Forest Landscape Integrity Index (FLII), which incorporates forest size, distance to edge, degree of fragmentation, and logging, with a range of 0 (most disturbed) to 10 (most undisturbed). Degraded forest was defined as cells with FLII scores from 0 to <7 (red) and intact forest as scores from 7 to 10 (green) using data generated by (Grantham et al., 2021). Oil palm is shown in purple. References for examples of hyperabundance: 1, Flemming *et al.* (2019); 2, Rae *et al*. (2014); 3, Valente *et al.* (2020); 4, Moore *et al.* (2022); 5, Shelton *et al.* (2014); 6, Meyer *et al*. (2009); 7, Taylor *et al.* (2016); 8, Melton *et al.* (2021); 9, Wilson & Edwards (2019).

Study species

I chose to focus on four pig and macaque species that have importance ecologically, culturally, and/or economically. These species are also the most frequently detected in camera trapping studies in Southeast Asia, together often accounting for >50% of detections: wild boar (*Sus scrofa*), bearded pig (*Sus barbatus*), pig-tailed macaque (*Macaca nemestrina*) and long-tailed macaque (*Macaca fascicularis*). These species possess several characteristics that make them prime candidates for reaching hyperabundance: they have generalist omnivorous diets, are found in disturbed forests, and exhibit rapid reproductive rates (M. F. Hansen et al., 2020; Ke & Luskin, 2019; Love et al., 2017; Luskin, Moore, et al., 2023; Luskin & Ke, 2017; Ruppert et al., 2018, 2022). These traits could potentially allow their populations to respond rapidly to changes in food, predation, and competition, and all four species are gregarious and group living and thus may be able to achieve higher densities than territorial solitary animals.

Establishing the population trends of pigs and macaques is imperative since they are linked to cascading impacts on the fauna and flora of local forest ecosystems, and human health and economics (C. G. Bueno et al., 2011; Cuevas et al., 2020; Gibson et al., 2014; Luskin et al., 2014; Luskin, Brashares, et al., 2017). Pigs (*Sus* spp.) and macaques (*Macaca* spp.) host high pathogen loads and are known to carry several diseases, including brucellosis, leptospirosis, Nipah, tuberculosis and Japanese encephalitis (discussed further in Section V.5). These species also share high rates of immune similarity with humans, with recent evidence of simian malaria outbreaks in Central Kalimantan, Indonesia (Barrios-Garcia & Ballari, 2012; Lee et al., 2011; Setiadi et al., 2016) acting as disease reservoirs and providing considerable potential for zoonotic disease transfer to humans (Gibb et al., 2020; Plowright et al., 2017; Shah et al., 2018).

Research questions and hypotheses

Here I investigate if abundance is related to environmental variables (e.g. elevation) or disturbance variables (e.g. edges, logging, oil palm). I hypothesize that (1) macaque abundance will be positively related to all types of habitat degradation since they are edge specialists and rarely hunted; (2) wild boar abundance will be unrelated to degraded habitats since they are edge specialists and are hunted to variable extents throughout the region; (3) bearded pigs will be negatively related to all types of degraded habitats since they are not considered edge specialists but are found in fragmented and logged forests and are actively hunted in their core range in Borneo; and (4) oil palm might be driving pig and macaque densities in nearby forests, as crop-raiding pigs have been argued to benefit from oil palm kernel food subsidies in three previous studies at the individual-landscape level and macaques are edge-specialist frugivores. For all relationships, I predict that macaques will show stronger associations to habitat measured at local scales (~1 km^2) and pigs at larger scales (20 km^2) because pigs are more vagrant and exhibit less site fidelity (Melletti & Meijaard, 2017). I also verify if habitat associations gleaned from camera trap detections are also present in independent studies estimating densities.

Methods

Approach

I used a multi-scale approach because these adaptable species may respond differentially to local and landscape-level factors and adjust their movements and home range sizes (M. F. Hansen et al., 2020; Thornton et al., 2011). First, I collated published density estimates to determine the drivers and absolute magnitude of changes in pig and macaque densities. Second, I utilized published camera trapping records to examine whether pigs and macaques show community dominance in degraded forests and near oil palm plantations at the landscape scale (comparing landscapes). Finally, I utilized new camera trapping records to test whether pigs and macaques became hyperabundant in degraded forests near plantations at the local scale (within landscapes).

Study area

My study area was defined as mainland Southeast Asia, Sumatra and Borneo for all landscape-level and camera-level analysis (Figure 5.2A), excluding Java, the Philippines and anything east of Wallace's line. This study area was selected to match areas that share relatively consistent natural habitat conditions with predominately evergreen tropical forests and include the native distributions of at least three of my four study species (see online supporting information, Figure S5.1).

For my landscape-level analyses of published densities and relative abundances in camera trapping, the exact sampling locations were obtained from the methods sections of published studies, or, when unavailable, I extracted coordinates from the study map (see Table S5.1 for density estimates and Tables S5.2 and S5.3 for relative abundance). If positional accuracy was a concern, I contacted the original authors for these details. Most camera trapping deployments covered large areas (10–1000 km^2) and were not arranged in a perfect grid or circle. To account for the lack of precision in identifying the exact sampling area centroids, I generated covariates describing the landscapes within a 20 km radius (1256 km^2) using Geographic Information System (GIS) zonal statistics in the spatial analysis software QGIS (see Table S5.4 for sources of covariates used in generating species abundance estimates; Figure S5.2). For the local-scale analyses from camera-level capture histories, I extracted covariates describing the areas within a 1 km radius (~3.14 km^2) of each camera. This distance was chosen as intermediate between the average home range size estimates for wild boars and macaques and has been used for studies focused on either genus (José-Domínguez et al., 2015; M. Rayan & Linkie, 2020).

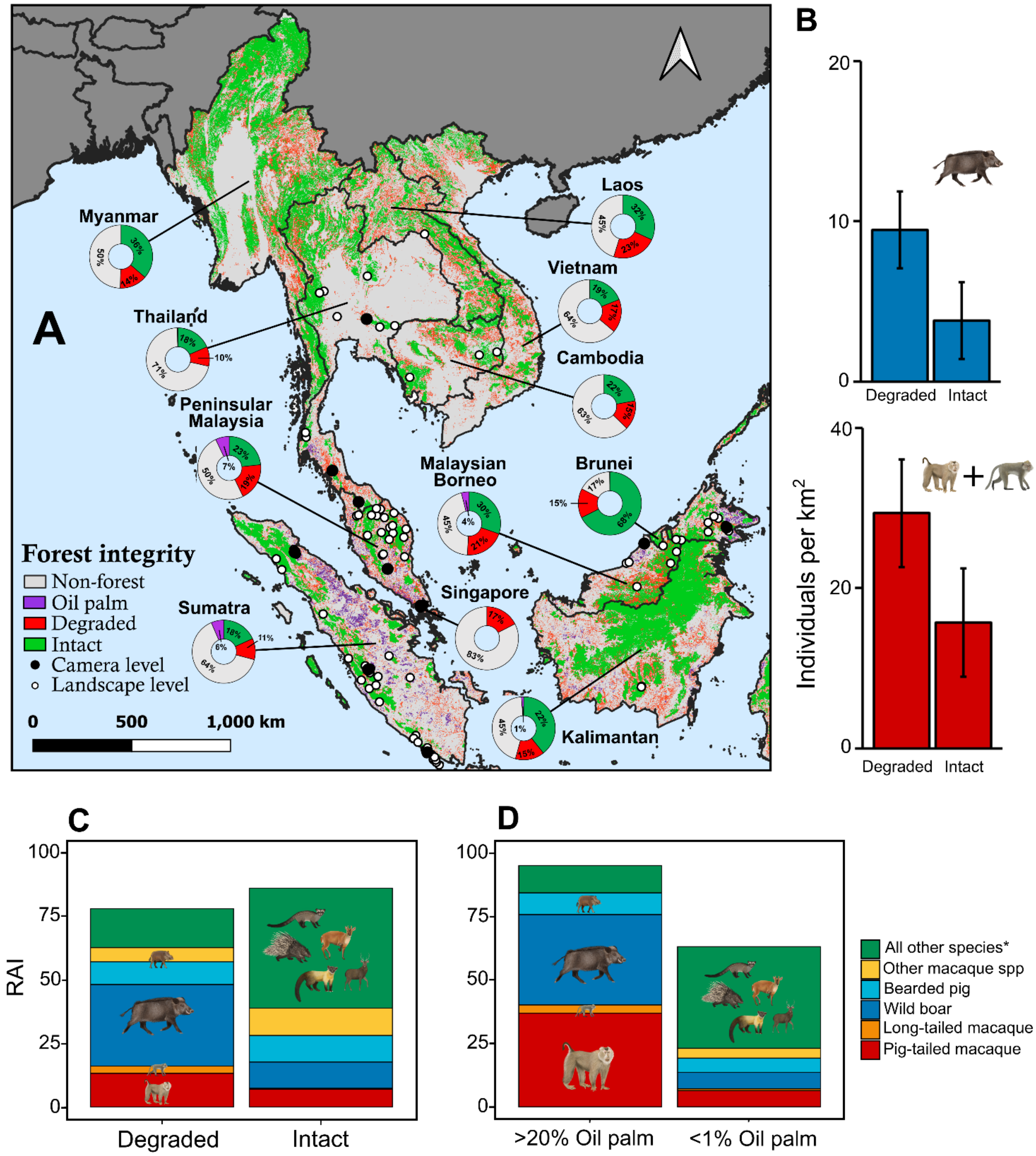


Figure 5.2. Study region and study sites within Southeast Asia (A), pig and macaque densities (B) and relative abundance index (RAI; independent photographs per 100 trap nights) in camera trapping studies (C, D). I compared RAI between degraded [Forest Landscape Integrity Index (FLII) 0 to <7) and intact landscapes (FLII 7–10) (C) and

between areas with high (>20%) and low (<1%) oil palm cover (D). In A, the doughnut charts depict the percentage of each landscape classification per country. B provides the mean ± S.E.M for 44 and 19 published density estimates of wild boar (top) and long-tailed and pig-tailed macaques (bottom), respectively, across the study region. In C and D, stacked bar charts show the average estimated RAI per species from 117 published camera trapping studies. *All other species includes 80 terrestrial vertebrates >1 kg. Statistical tests and box plots for B–D are presented in Figs S4–S6.

Extracting standardized covariates to describe study areas

I focused on two covariates in testing the underlying drivers of pig and macaque hyperabundance and/or community dominance (Table S5.4). I used the Forest Landscape Integrity Index (FLII) values with 300 m pixel resolution to assess the influence of habitat degradation (edges, fragmentation, and logging; Grantham *et al.*, 2021). The FLII (hereafter ‘forest integrity’) is a globally consistent landscape-level index that incorporates forest loss, logging, and edges, as well as inferred effects from fragmentation and the loss of connectivity and is scaled between values of 0 = most degraded to 10 = most intact. Next, I quantified the percentage cover of oil palm in my study landscapes using the CRISP 2015 land cover map of Southeast Asia (Miettinen et al., 2016). This GIS layer includes 18 landscape types (including oil palm) at 250-m resolution.

There are various benefits and errors when integrating spatial covariates from many studies into standardized and consistent GIS layers. In particular, there may be some inaccuracies when extracting covariates from older studies (pre-2010) using GIS layers created after 2015, especially for the dynamic landscapes of Southeast Asia. However, the GIS layers I used rely upon numerous remote-sensing images obtained over multiple years and are the most robust sources currently available. For example, a pre-2010 study in an intact forest landscape may have suffered extensive clearing and oil palm establishment since 2010, and thus my method may incorrectly describe these coordinates as degraded with oil palm, when in fact at the time it was intact forest. Given recent ongoing clearing outpacing any reforestation in the study region, the direction of this bias is almost always to overestimate disturbance-sensitive species’ presence in degraded areas, which reduces my statistical power. As a result, I likely underestimate true effect sizes, thereby yielding results that should be considered conservative.

Macaques and wild boar density estimates

I collated published densities of pigs and macaques using a *Web of Knowledge* search performed with the search terms including common and scientific names AND dens* AND

Asia. I also investigated citations within the identified papers for density estimates and included any suitable papers. This resulted in 23 density estimates for macaques (9 for pig-tailed macaques and 14 for long-tailed macaques), across 13 landscapes from 14 publications. I found a total of 79 density estimates for wild boar across 41 landscapes from 47 publications; there were no bearded pig density estimates so they were excluded from this analysis (Table S5.1). I estimated mean densities in intact and degraded forests using linear mixed-effects models (LMMs) with the R-package *lme4* (Bates et al., 2015), with landscape included as a random effect to account for multiple observations from the same area. As there are relatively few density observations for macaques, I grouped pig-tailed and long-tailed macaques (same genus and with similar diets/behaviour) and included both species and landscape as random effects (Table S5.5). I feel it is appropriate to pool these two species in this analysis. I note that the original density estimates did not all employ standardized sampling or analytical methods and this could introduce additional noise.

Pig and macaque abundance among landscapes

I examined the landscape-level predictors of pig and macaque abundance using capture rates from published camera trapping studies in Southeast Asia (Figure 5.2C, D). I identified published camera trapping studies using a *Web of Knowledge* search performed with the criteria “camera trap” AND any of my study countries, as well as Asia*, Malay*, Thai*, Sumatr* and Born*. I also performed the same search in *Google* to locate grey literature and academic theses. I retained studies that used unbaited camera deployments in forest, and which reported the full species capture lists (number of independent photographs of all mammals >1 kg) and the trapping effort (trap nights) (Tables S5.2 and S5.3). I refer to the area sampled as a ‘landscape’, which was usually a national park, production forest, or collection of nearby forest patches, and my final sample size was 164,055 detections of 89 species from 43 studies and 58 landscapes. I used 20-km radius buffers to extract landscape covariates providing average forest integrity values and landscape-scale percentage oil palm cover. I used published camera trap data to assess relationships between pig and macaque capture rates and landscape covariates (forest integrity and % oil palm cover). I used generalized linear mixed models (GLMMs) with the number of independent captures as the response variable (count data, assuming Poisson distribution), controlling for sampling effort as a model offset, and including ‘landscape’ as a random effect. Significance was assessed using the z-value and Satterthwaite approximations for degrees of freedom using *lmerTest* in R (Kuznetsova et al., 2017). Since I make comparisons within species and using similar sampling protocols, I assume that detectability does not vary systematically with my covariates, and therefore infer that differences in capture rates reflect true differences in abundance. I also used relative abundance index (RAI) from the published camera trap data to run LMMs to assess community dominance of pigs and macaques. My RAI comparisons were performed by separating forest integrity into two groups [high (values 7–10) and low forest integrity (0 to < 7)] and separating oil palm landscapes into high (area >20%) and low oil palm cover (area <1%), and I ran separate LMMs for all four pig and macaque species.

Local pig and macaque abundance within landscapes

I conducted 20 new camera trapping sessions in 10 landscapes in Thailand (two sites), Peninsular Malaysia (two sites), Singapore (one site), Sumatra (three sites) and Borneo (two sites) to assess the effects of local habitat characteristics on relative abundances (see Table S5.6 and Appendix S5.1 for site description and trap deployment details). I produced detection history matrices using the total number of individuals detected within a sampling occasion of 3 days to reduce zero-inflation, and spatially resampled all cameras into hexagonal grid cells of equal size (0.86 km^2, hereafter ‘sampling units’) to satisfy spatial independence (Figure S5.3; see Appendix S1 for detailed methods; Rayan & Linkie, 2016). Habitat covariates were averaged when there were multiple cameras within the same cell. I used hierarchical N-mixture (NM) models to estimate the relative abundance of pigs and macaques while accounting for imperfect detection using the *pcount()* function in *unmarked* in R (Fiske & Chandler, 2011; Royle, 2004). NM models provide an unbiased relative abundance metric (hereafter ‘estimated abundance’), allowing for robust comparisons across multiple surveys for species that cannot be identified individually (Royle, 2004). I included ‘landscape’ as a fixed effect to account for three landscapes sampled over multiple trapping sessions and included sampling effort as a fixed effect on the detection probability formula to account for multiple cameras in the same grid cell (Table S5.7). I ran the same NM models for all species and tested if estimated abundance varied with forest integrity and percentage of oil palm plantations within 1 km of each camera.

However, it is important to highlight potential assumptions of the NM modelling that could be violated such as potential double counting of individuals (Link et al., 2018; Nakashima, 2020) within the 3-day sampling interval I chose. A potential solution suggested by (Nakashima, 2020) is to use a detection formula with a Poisson distribution instead of the normal binomial distribution in regular NM models. The idea is that it changes detection probability away from detecting the species if it is present, and instead the probability of detecting the individual of the species if it is present. This method was tested by a colleague for his co-abundance modelling predator-prey paper interactions paper (Amir, Sovie, et al., 2022), which after discussions I ultimately decided to avoid using the Poisson formula. While it did generate smaller (and probably less biased) population density estimates, it produced almost exactly the same trends as the normal NM model when examining relationships with covariates. Moreover, the only way to implement the Poisson detection formula is to manually code it, as there are no packages that run this analysis (at least at the time the analysis was being performed).

Another key assumption in NM modelling is that all individuals of a species have equal detection probability among the population, however the assumptions in NM populations can be biased. This assumption appears to be untested as of yet due to the difficulty with unmarked animals. I believe NM models are good for group-living animals because the count of individuals give variation in to the count matrix that can later be attributed to covariates. For example, when occupancy is very high across all sites, we might not see any differences due to covariates, but when we look at abundance that is informed by counts of individuals, we could see a range from 1 to N, thus providing more nuance in the relationship that would be obscured with occupancy modelling.

In conclusion it’s important to realise that NM models are fraught with assumptions that are easily violated with camera trapping data. However, it’s probably the best option we have for single-species models that correct for imperfect detection. The key to avoiding many of the issues with these assumptions is to carefully interpret the results, focusing on directional change in species abundance relative to covariates and not as absolute population sizes. I also used other datasets RAI and density estimates along with other analytical methods to see if similar directional trends were detected which could back up the NM modelling results.

Results on hyperabundance in Southeast Asia

Densities

Population densities of wild boar were 148% higher (LMM: $t_{50.1} = -2.35$, $p = 0.023$) in degraded landscapes (mean ± S.E.M = 9.5 ± 1.9 individuals/km^2) compared with intact landscapes (3.8 ± 2.4 individuals/km^2) (Figure 5.2B; see Figure S5.4 for results of statistical tests). Macaques (both species combined) were 87% higher (LMM: $t_{15.2} = -2.03$, $p < 0.059$) in degraded landscapes (29.4 ± 5.9 individuals/km^2) compared with intact landscapes (15.7 ± 6.7 individuals/km^2) (Figure 5.2B). Pig-tailed macaques, when considered separately, showed densities 69.7% higher in degraded landscapes (24.1 ± 6.7) compared with intact landscapes (14.2 ± 0.7) (LMM: $t_2 = -13.33$, $p < 0.005$; Table S5.5). Long-tailed macaques could not be modelled separately due to insufficient data from intact forest sites for a statistical test but the mean density for degraded landscapes was 520% higher with 31 individuals/km^2 compared to 5 individuals/km^2 for intact forest.

Community dominance

When comparing communities from intact *versus* degraded forest landscapes, the community dominance of pigs and macaques (i.e. the total RAI of the four focal species) rose from 32.7% to 73.2% of all independent captures, and when comparing low (<1%) to high (>20%) oil palm cover, the community dominance of pigs and macaques rose from 30.4% to 88.7% (Figure 5.2C,D; see Tables S5.8 and S5.9 and Figures S5.5 and S5.6 for data from individual species). These shifts in community dominance were driven both by higher detection rates of the four generalist species and lower detection rates of forest specialists (Figure 5.2C, D). In fact, pooled detections of the other 85 wildlife species > 1 kg were 63.9% lower in degraded landscapes (LMM: $t_{65} = 2.95$, $p < 0.004$; Figure 5.2C) and 75.5% lower in high (>20%) oil palm cover landscapes (LMM: $t_{56} = 2.88$, $p < 0.005$; Figure 5.2D).

Landscape-level determinants of hyperabundance

When examining habitat relationships using Poisson GLMMs with detections as a response variable and the continuous landscape-level predictors I found strong but not entirely consistent patterns. Long-tailed macaques showed a negative relationship with forest integrity (GLMM: $z = 5.81$, $p = 0.002$), while bearded pigs showed a significant positive relationship with forest integrity (GLMM: $z = 3.94$, $p = 0.008$). There were no significant relationships between forest degradation and wild boar or pig-tailed macaques (Figure 5.3C). Relationships between the percentage oil palm in the landscape and wild boar and long-tailed macaque abundance were significantly positive (GLMM: $p < 0.01$ for both species) while no significant relationship was found for pig-tailed macaques or bearded pigs (Figure 5.3D).

Local determinants of hyperabundance

At the local scale, the estimated abundance from NM models was higher for three of the four species when sites with the minimum and maximum observed forest degradation were compared: wild boar = +196% (95% confidence interval (CI) = 195.6–197.3%), long-tailed macaque = +456.7% (95% CI = 437.4–476.7%) and pig-tailed macaque = 62.9% (95% CI = 62–63.9%; all NM: $z = <–5$, $p < 0.0001$) (Figure 5.3A). However, abundance was 77.8% (95% CI = 76.3–79.3%) lower for bearded pigs at the most degraded sites ($z = 8.5$, $p < 0.0001$; Table S5.7). Estimated abundance was higher for all four species when comparing between landscapes with the minimum (<1%) and maximum (>60%) observed oil palm cover [wild boar = +336.7% (95% CI = 306.5–369.3), bearded pig = +655.3% (95% CI = 571.1–750.1), long-tailed macaque = +9036.8% (95% CI = 8899.8–9175.9%), pig-tailed macaque = +447.3% (95% CI = 426.6–468.7; all NM: $z = >15$, $p < 0.0001$; Figure 5.3B; Table S5.7].

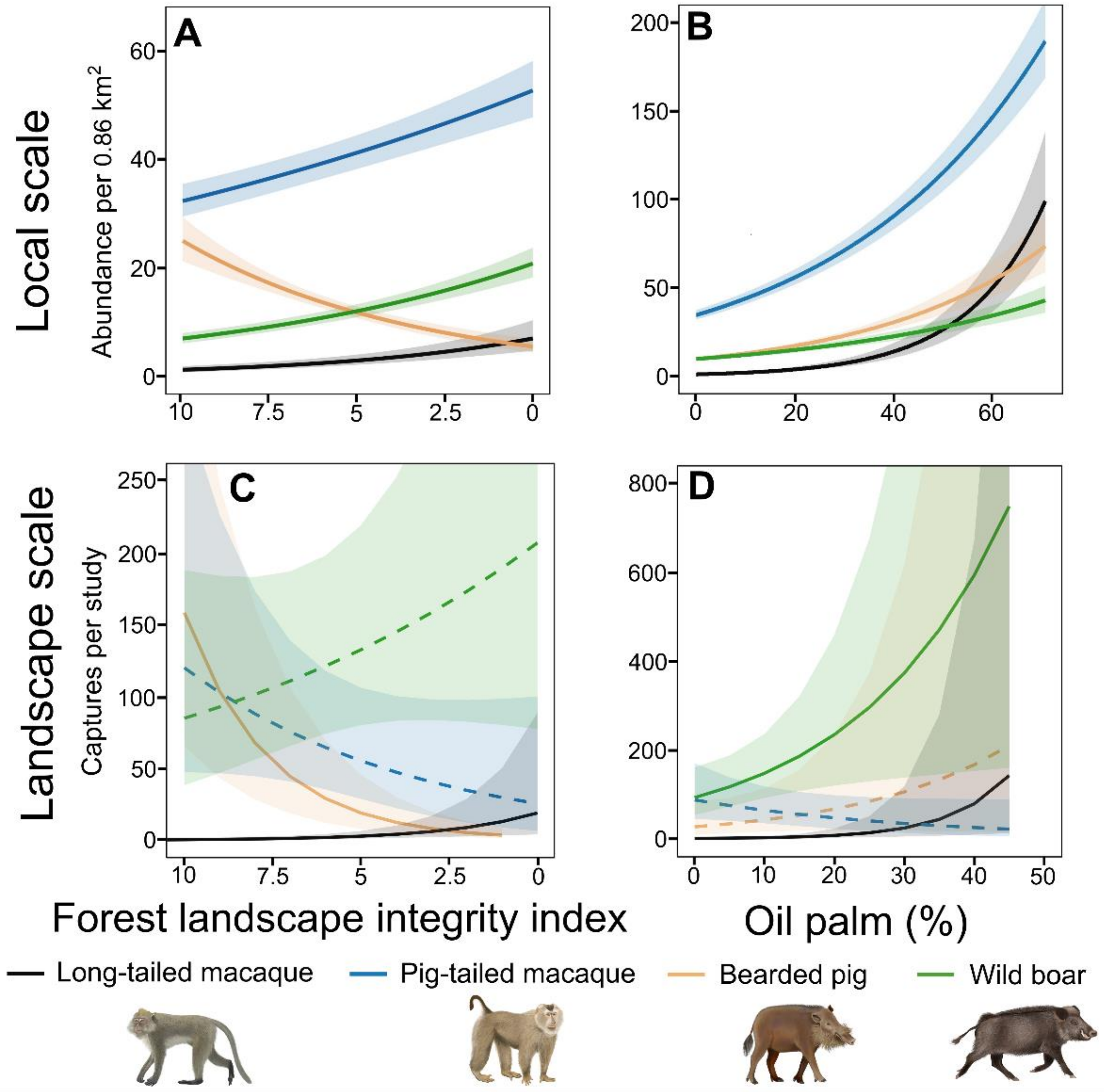


Figure 5.3. Pig and macaque abundance in relation to forest integrity and oil palm agriculture in the landscape. The local-scale panels (A, B) show estimated abundance per 0.86 km^2 hexagonal grid cell across 10 newly sampled landscapes in Southeast Asia from N-mixture detection-corrected hierarchical modelling with covariates measured within 1 km of each camera. The landscape-scale panels (C, D) show estimated detections per study from generalized linear mixed models (GLMMs) with covariates averaged over 20 km radius study areas (N = 117 published data sets). Solid lines indicate a significant trend ($p < 0.05$), and shaded regions show 95% confidence intervals. Note forest integrity is descending so that intact landscapes are on the left and more degraded landscapes are on the right.

Discussion

The causes and consequences of hyperabundance

I document the hyperabundance of pigs and macaques across Southeast Asia. The *Sus* and *Macaca* genera now comprise the majority of all terrestrial vertebrates detected on camera traps in disturbed forests, constituting 73.2% and 88.7% of all captures in degraded forests and landscapes with >20% oil palm cover, respectively. These results show strong community dominance. Examples of hyperabundant native generalists can be found globally, including baboons in Africa, mesopredator release in North America and deer and pig species in Europe. Hyperabundance is often triggered by a reduction in top-down control by native predators, or by the presence of food subsidies, especially for disturbance-tolerant species and high-fecundity species (Flemming et al., 2019; Luskin, Brashares, et al., 2017; Rae et al., 2014; Valente et al., 2020).

Based on my definition of hyperabundance in mammals, describing the elevated numbers of Southeast Asia's pigs and macaques as hyperabundance is warranted for several reasons. First, my comparisons are limited to habitats that are predominantly tropical evergreen forests and include many observations from the same landscapes. Second, my study includes observations extending over more than 20 years, suggesting the observed trends are not ephemeral. Third, neither pigs nor macaques fit cleanly into either *r*- or *K*-selected life histories. Compared to similarly sized species, pigs are able to reproduce rapidly producing up to two large litters per year under ideal conditions with plentiful resources (Bywater et al., 2010; Croft et al., 2020) while also being comparatively long-lived (Fryxell et al., 2014). Fourth, I identify *in situ* anthropogenic environmental drivers including habitat degradation and food subsidies from oil palm plantations as deviations from natural long-term conditions.

Degraded forest and agricultural food subsidies

At the landscape scale, habitat associations with forest degradation were unclear for wild boar and pig-tailed macaques, whereas long-tailed macaques performed better in degraded landscapes and bearded pigs performed worse. High oil palm coverage (>20%) elevated the abundance of both wild boar and long-tailed macaques. Densities at the landscape scale were also higher in degraded habitats for both wild boar and macaques. At the local scale, which considered the 3.14 km^2 areas around cameras, habitat degradation and oil palm cover were consistently associated with elevated population abundance of wild boar and macaques. The positive association between bearded pigs and forest integrity, both within and across landscapes, may suggest a preference for primary forest adjacent to oil palm plantations. This is supported by a previous study in Borneo showing that bearded pigs utilize oil palm landscapes but prefer adjacent forested areas for a wider range of their behaviours (Love et al., 2017). Taken together, my results likely reflect both that degraded areas have higher densities of pigs and macaques, and that mobile individuals (and groups) within these landscapes prefer edges near oil palm, as opposed to forested areas further from edges.

My results documenting the highest pig and macaque densities near oil palm plantations align with other work in Malaysia showing abnormally high wildlife abundances within forest fruit gardens (J. H. Moore et al., 2016). This suggests that supplementary food can release wildlife from natural bottom-up regulation imposed by resource scarcity, which may be especially important in Southeast Asian forests where the fruiting phenology of most canopy trees shows a supra-annual masting cycle (Curran & Leighton, 2000). Only certain habitat-generalist species can access food subsidies beyond forest edges, such as those provided by oil palm plantations, so there may be asymmetric competition with other herbivores. Habitat and dietary generalists such as pigs and macaques that thrive in ecotones frequently raid cultivated crops, and consume both native plant material and human refuse from farmers living within oil palm landscapes (Barrios-Garcia & Ballari, 2012; Bieber & Ruf, 2005), likely out-competing deer, tapirs, and other vertebrate herbivores and omnivores in these degraded habitats.

Other factors supporting hyperabundance

There are three other reasons for the success of pigs and macaques in degraded forest landscapes. First, both pigs and macaques have high fecundity, allowing them to exploit resources rapidly, tolerate hunting pressure, and recover quickly from disturbances. Second, large mammalian predators often avoid degraded habitats and oil palm, indirectly benefitting prey species capable of exploiting those same areas (Brodie et al., 2015; Luskin, Albert, et al., 2017). Third, pigs and macaques are rarely targeted by hunters throughout regions where Islamic religious practices are observed, since the Halal diet forbids pork and fanged animals, including macaques (Luskin et al., 2014). The exception is areas in Borneo occupied by the Dayak people who often hunt bearded pigs (Kurz et al., 2021, 2023; Luskin et al., 2014).

Consequences of wildlife hyperabundance for forests

My findings have important conservation implications. Hyperabundant omnivorous ungulates and primates can alter vertebrate food webs through direct predation of smaller animals such as rodents, reptiles and birds (Ruppert, Mansor & Shahrul Anuar, 2014; Ruppert *et al.*, 2018; Law, Ruppert & Holzner, 2018), disturb nesting sites (Mori et al., 2021), exert exploitative competition of a shared resource (Barrios-Garcia & Ballari, 2012; Ilse & Hellgren, 1995) and induce indirect effects through degradation of understory structure (Luskin et al., 2019; Luskin, Johnson, et al., 2021; Mori et al., 2021). Altered understory structure occurs through intense soil disturbance and direct seed/seedling predation (C. G. Bueno et al., 2011; Cuevas et al., 2020) and promotes the spread of invasive plant species (Fujinuma & Harrison, 2012), facilitates liana proliferation on host trees (Luskin et al., 2019), and alters tree diversity (Luskin, Brashares, et al., 2017; Luskin, Johnson, et al., 2021). Further, pig soil disturbances in their invasive range are thought to impact carbon storage potential by driving greenhouse gas emissions representing up to 0.4% of annual land-use and forestry emissions (Chanthorn et al., 2019; Dirzo et al., 2014; O'Bryan et al., 2021; Terborgh & Estes, 2013), and there is little reason to suggest that their hyperabundance within native ranges would not produce similar levels of emissions. The sustained hyperabundance of pig and macaque populations in degraded forests and near oil palm plantations may deplete natural forest tree seeds during a mast, thus reducing seedling recruitment and future forest regeneration, and thereby undermining the strategy of predator satiation (Curran & Leighton, 2000; Janzen, 1974; Jia et al., 2018; Luskin et al., 2019; Luskin, Johnson, et al., 2021; P. J. Williams et al., 2021). The influence of hyperabundant macaques on biotic communities is less well understood, but I note that their seed-dispersal capacity appears to be limited for large-seeded plant species (Nakashima & Sukor, 2010).

Consequences of wildlife hyperabundance for humans

The hyperabundance of pigs and macaques also has important impacts on humans, since they drive economic damage from crop-raiding and display highly aggressive behaviour towards humans, even in urban settings (Balasubramaniam et al., 2020; Ilham et al., 2017; Luskin, Brashares, et al., 2017; Priston & McLennan, 2013). Pigs are an amplifying host in which zoonotic viruses can modify for transmission to humans, whereas macaques can act as both reservoirs and amplifiers. The rise of pigs and macaques has been implicated in a higher potential for zoonotic disease transmission (Gibb et al., 2020). For instance, zoonotic diseases such as malaria *Plasmodium knowlesi* have a geographic range limited by their mosquito vectors and simian hosts (Moyes et al., 2014), but as landscapes become increasingly degraded zoonotic host populations both expand and also increase their proximity to humans, elevating disease risk. This is evident in Malaysian Borneo where human malaria outbreaks – mediated by macaques as zoonotic carriers (Fornace et al., 2016) – have increased. Cases of the zoonotic disease monkeypox have increased throughout 2022; this virus was first named and classified from samples taken from long-tailed macaques in Denmark in 1958 (Liu et al., 2022; Magnus et al., 2009). Nipah is spread by wild boars in Malaysia and Singapore (Yu et al., 2018), and tick-borne disease transfer from wild boars occurs in Europe (Castillo-Contreras et al., 2022; Hrazdilová et al., 2021). Both species also carry a variety of helminths (e.g. parasitic worms) that plague human health in developing countries. Domestic livestock are also threatened by disease transfer from pigs, including African swine fever and foot-and-mouth disease (Denstedt et al., 2021).

Managing hyperabundant wildlife

Hyperabundant species can impact humans and local fauna and flora in a multitude of negative ways, requiring extensive control measures (J. H. Moore et al., 2022; Taylor et al., 2016; Wilson & Edwards, 2019). There are significant efforts to manage hyperabundant pig and macaque populations in Malaysia, Singapore and Indonesia (Lamperty et al., 2023; Luskin et al., 2014). Population control through cage trapping, culling, hunting and sterilization may be effective when adequate resources are available (Croft et al., 2020; Luskin et al., 2014; Priston & McLennan, 2013). However, the high fecundity of these species makes control difficult as success (e.g. >50% population decline) would require high-intensity management for prolonged if not indefinite periods (Annapragada et al., 2021). Management efforts to limit pig and macaque access to oil palm have largely failed. Luskin *et al.* (2017b) describe an attempt by the FELDA oil palm company to prevent wild boar from killing oil palm seedlings in Peninsular Malaysia. They constructed a 1 m trench with 1.5 m solid metal sheeting mounted vertically above the trench and stretching along approximately 5 km of the forest-plantation edge. Within weeks the trench had flooded, the pigs enjoyed these areas as pseudo-wallows, and then they dug underneath or pushed over the compromised fence. Macaque species can similarly negotiate fencing with ease (Mysterud & Rolandsen, 2019). Likewise, as semi-natural buffer zones between forests and plantations are also likely to be advantageous for pigs and macaques, such 'designer landscapes' are unlikely to improve the situation (Koh et al., 2009; Reidy et al., 2008). Another focus should be on limiting further oil palm expansion into surrounding intact forests, and instead exploiting already disturbed areas (Luskin & Potts, 2011). Long-term monitoring data focused on species abundance are essential to assessment of baseline population levels and of the effectiveness of ongoing management techniques. In the meantime, I recommend the prevention of future development of agriculture within close proximity to intact forests which could provide food subsidies to generalist species.

The roles of predators, competitors, and hunting

The role of hyperabundant native generalists in providing supplementary prey for carnivores has received little attention, nor has the role of hyperabundant native generalists on competitors, except for rodents on island fragments in Thailand (J. H. Moore et al., 2022). Likewise, there is little known regarding the role of hunting in controlling pig and macaque populations, although this has been attempted for macaques in Peninsular Malaysia, and Dayak hunters in Sarawak nearly extirpated bearded pigs from a small forest adjacent to oil palm (Harrison et al., 2016). Especially poignant in the region is the role of religion and culture in shaping hunting, wildlife abundance, and cascading impacts on forest ecology (Kurz et al., 2021, 2023). Further research should also focus on the potential cascading impacts imposed by hyperabundant pigs and macaques in Southeast Asia, including their effects on vegetation structure, faunal communities, and human–wildlife conflicts. There is also an urgent need to improve disease monitoring of these species in this region, especially at edges where they are most likely to interact with domestic animals and humans. Further work on the top-down control of pigs and macaques is required to understand fully the mechanisms driving hyperabundance of generalist species in tropical forest regions (Amir, Sovie, et al., 2022; Hendry et al., 2023).

Caveats

Some trade-offs were required in collating this data set for larger Asian vertebrates to make regional inferences. Data sources vary in quality and in the methodology used to generate the values I included in my synthesis. I sought to overcome this by triangulating results using different forms of analysis to increase confidence in the trends reported. I advise that conditions may change rapidly due to disease (e.g. African swine fever), changes in harvesting (macaque capture for medical testing) or lethal management. For example, both *S. scrofa* and *S. barbatus* populations have crashed recently due to African swine fever outbreaks across the region (Luskin, Moore, et al., 2023). The rapid spread of this disease could have been aided by the high population densities reported here.

Conclusions

(1) The wildlife origins of the COVID19 pandemic and alarming recent work (Gibb et al., 2022) show that generalist mammals persisting in human-modified ecosystems often host high pathogen loads and pose serious zoonotic disease risks, emphasizing the importance of new research in these areas.

(2) I reviewed the evidence for two key generalist groups in Southeast Asia, a biodiversity and zoonotic disease risk hotspot. Specifically, I examined population trends for pigs and

macaques, which are known zoonotic disease reservoirs. I show that these species are more common in most degraded areas, but the most pronounced increases – to a level I consider hyperabundant – were contingent on the nearby presence of oil palm agriculture in the landscape. This supports a dominant role of food subsidies in shaping wildlife outcomes, as opposed to increased foraging in degraded forest habitats. These results are likely generalizable, as similarly coupled human–natural environments abound across the globe (Goheen, 2016).

(3) These results can inform conservation and epidemiological work in Southeast Asia, and my approach can be replicated for other species and regions.

Chapter 6 : General conclusion

The dawn of generalists in a changing world

This thesis tells the story of a rapidly evolving world wherein the present moment signifies the era of generalists. The tropics, which have managed to remain relatively intact until recent decades, are showing similarities to what occurred in temperate regions hundreds of years ago. The simplification of these landscapes led by preindustrial deforestation caused extensive declines in native fauna (Kaplan et al., 2009). Now this phenomenon is repeating itself in the tropics.

Human landscape alterations are a key factor contributing to global species declines (Bregman et al., 2014; Dirzo et al., 2014; Torres-Romero et al., 2023) and are a driving force of the Earth's ongoing sixth mass extinction (Barnosky et al., 2011; Pimm et al., 2014). The rapid rate at which ecosystems are changing is a challenge for species which respond in vastly different ways depending on their life history traits (Table 5.1), making it extremely difficult for most species to adapt, especially forest specialists (Filgueiras et al., 2021; Tabarelli et al., 2012). Habitat fragmentation now permeates almost every landscape on Earth (Haddad et al., 2015; Kennedy et al., 2020), and is a major concern for conservation efforts, linked to extensive species loss globally (Fischer & Lindenmayer, 2007; Foley et al., 2005). Oil palm landscapes, which are a newly formed energy rich habitat, now replace extensive areas formally occupied by old growth forest (Descals et al., 2021; Vijay et al., 2016). These new habitats offer beneficial opportunities for a select group of species which possess the correct combination of life history traits (Filgueiras et al., 2021; J. H. Moore et al., 2023) but generate costs for the surrounding ecosystems in the form of cascading ecological impacts (Luskin, Brashares, et al., 2017). This thesis represents an effort to expand knowledge on the ecological implications of human modified landscapes, focusing on the effects of energy infrastructure and agriculture, which are two of the most important drivers of biodiversity loss in the tropics.

Chapters 2-5 reveal an overarching theme: the importance of species traits in determining the long-term survival and even dominance of a species in a rapidly changing world. Although this thesis does not examine individual traits implicitly, it is evident that species with generalist characteristics fair extremely well in degraded human-modified landscapes (Filgueiras et al., 2021; Finn et al., 2023). However, most species found within tropical forests are specialists in nature, adapted to exploit the diverse array of niches available in pristine forest habitats (Haddad et al., 2015; Maxwell et al., 2016). This specialization, however, has become a major disadvantage in a world experiencing rapid loss of complex habitat, causing disproportionate declines mediated by functional traits such as larger body sizes, slow reproduction, limited dispersal capacity, specialized diets and narrow niche breadths (Betts et al., 2017; Fritz et al., 2009; Henle et al., 2004; Newbold et al., 2014; Slatyer et al., 2013).

In contrast, the study species (*Rattus* spp, *Macaca* spp and *Sus* spp) addressed in this thesis that thrived in degraded landscapes shared similar species traits: an extreme tolerance to human proximity, high fecundity, adept dispersal capabilities and opportunistic diets (Gibson, 2011; M. C. Hansen et al., 2020; Love et al., 2017; Luskin, Brashares, et al., 2017; Terborgh & Estes, 2013). In fact, some of these species were capable of exploiting human-modified landscape so well that they attained hyperabundant populations (J. H. Moore et al., 2022, 2023).

Limitations of the species-area relationship and island biogeography theory

The results of Chapters 2, 3 and 4 also demonstrated some key limitations of the equilibrium theory of island biogeography theory (ETIB) (MacArthur & Wilson, 1963; Preston, 1962), displaying breakdowns in the species-area relationship (SAR), one of the most well-known and widely detected ecological patterns (Lomolino, 2000b). Extinction debts were also found to have been paid at faster rates than previously expected (Diamond, 1972; Jones et al., 2016). Two predictor variables, habitat degradation and dominance of an invasive rodent, were found to have considerable explanatory power for richness declines over traditional variables such island size and isolation distance.

Although habitat degradation has the potential to cause significant negative impacts to the resident animal community, this variable has rarely been accounted for in models such as ETIB or SARs (Benchimol & Peres, 2015b; Lomolino, 2000b; Neto et al., 2022). The results from both Chapter 3, which examined the effect of habitat degradation on the small mammal community and Chapter 4, which examined the effect of habitat degradation on the terrestrial vertebrate community including birds, showed that habitat degradation was an important predictor of species decline within insular fragmented landscapes, particularly for terrestrial vertebrates. This phenomenon was not limited to a single group but was demonstrated for multiple levels of the animal community.

Additionally, the ETIB and SARs rarely account for the potential negative impacts of other fauna on the richness of native species such as the presence of hyper-dominant rat species, which have been found to cause significant declines to native species globally when introduced to islands (Harper & Bunbury, 2015). Chapter 2 demonstrates that a generalist rat, which can reach hyperabundant levels, caused significant declines in the native small mammal community, completely overriding the species-area relationship. Utilizing a long-term dataset, following the trajectory of small mammals isolated 33 years prior, Chapter 2 also revealed that a hyper-dominant rat was responsible for the decline in native small mammal richness faster than expected by extinction debt alone. Chapter 3, which assessed species diversity of the small mammal community across multiple landscapes, also demonstrated significant negative effects on native small mammal species richness induced by the hyper-dominance of *Rattus* spp, further confirming the limitations of the ETIB framework in explaining trends within insular fragmented islands.

In conclusion, Chapters 2-4 demonstrate the importance of including other explanatory variables alongside well-established ecological models such as ETIB and SARs, to explain changes in animal communities. Modern ecology is dealing with the task of understanding how animals cope within a rapidly evolving landscape through large-scale fragmentation, a process causing unpredictable cascading effects requiring more complex explanatory models, particularly given frequent synergistic interactions between co-occurring environmental stressors, such as habitat loss and bioinvasions, (e.g. Laurance & Peres, 2006).

Agricultural food subsidies and their role in nature

Chapter 5 delves into the ecological impact arising from the cultivation of oil palm, the rapid increase in pig and macaque populations, and their interactions within the surrounding landscape. This chapter demonstrates that generalist species are capable of thriving in degraded and oil palm landscapes compared with other animal species. Oil palm plantations, which are newly formed energy rich landscapes, prove to be the most beneficial to two groups of animals: macaques and wild pigs, reaching hyperabundant levels and high densities. This phenomenon is likely due to the difference between the energy content of oil palm plantations and natural forests which in Southeast Asia typically follow a mast fruiting reproductive strategy whereby entire tree communities' fruit synchronously every 2-5 years, in between which food availability is limited (Curran & Leighton, 2000; Malhi et al., 2022). Any species capable of accessing this limitless food source is no longer bound by the constraints of the natural forest, and subsequently can reproduce rapidly all year round.

Ecological implications, global context, and conservation lessons

Similar responses to human-modified landscapes as seen by animal species in Southeast Asia are likely to be occurring elsewhere globally, as evident in many studies demonstrating hyperabundance in disturbance-tolerant species in countries around the world (Flemming et al., 2019; J. H. Moore et al., 2023; Rae et al., 2014; Valente et al., 2020). These hyperabundant species cause cascading effects within ecosystems, inducing ecological damage (Estes et al., 2011), modifying plant and animal community structures (Dirzo et al., 2014; Ivey et al., 2019; Terborgh & Estes, 2013), often leading to a variety of human-wildlife conflicts; crop damage (Luskin et al., 2014; Taylor et al., 2016; Wood & Fee, 2003), and property damage (Barrios-Garcia & Ballari, 2012). These hyperabundant species can even drive down the richness of native species (J. H. Moore et al., 2022) and in the worst case scenario this can lead to an ecosystem wide ecological meltdown (Terborgh et al., 2001).

This work reveals a shift in the balance of species within ecosystems as humans modify landscapes for their own needs and forewarns similar impacts globally, as hydropower and oil palm both expand in Africa and South America (Elagib & Basheer, 2021; Flecker et al., 2022; Medina et al., 2019; Pirker et al., 2016). While evidence of invasive species such as *Rattus* proliferating within insular fragmented landscapes induced by hydropower dams in South America is somewhat limited, my research demonstrates the potential devastating impacts that may occur in the future, as isolated insular fragments seem to be less resistant to the establishment, and subsequent dominance of an invasive species. As I show in this thesis, this is especially evident when the presence of invasive species is compounded by habitat degradation.

As fragmented landscapes created by hydropower dams benefit the generalist *Rattus* species, oil palm plantations also promote the increase of certain generalist native species abundance. Although the documented increase of native primate and pig species might appear as a positive outcome of this kind of land use change, my results show that a large proportion of the animal community are incapable of utilizing oil palm habitat. Thus, despite benefitting a limited number of generalist native species, just like hydropower dams oil palm also leads to the simplification of native animal communities. Not only because of the direct negative effects of oil palm plantations, but also because of the cascading effects caused by the increase of both pigs and macaques in adjacent forests. It is possible however, that the hyperabundant phenomenon seen in Southeast Asia, as documented in this thesis, is less likely to occur in Africa and South America. Although food subsidies that favor the conversion of native forest into oil palm plantations are also present in Africa and South America, masting events are not a characteristic of these regions. This means that the faunas of African and South American forests are not subject to the periods of food scarcity that the fauna of Southeast Asian forests face in the years following masting (Curran & Leighton, 2000; Malhi et al., 2022). Thus, the resources that palm oil plantations offer to these animals will be a less determining factor for the survival and explosion of their populations.

This thesis demonstrates the critical conservation importance of maintaining highly intact, pristine landscapes to preserve the baseline equilibrium of animal communities. Little conservation value resides within fragmented insular islands or within mono-culture oil palm plantations. Efforts should be made to ensure that a landscape wide assessment is made on the future impacts of the establishment of new hydropower dams and for the expansion of oil palm plantations. Conservation recommendations for oil palm expansion include prioritizing existing landscapes which have already experienced extensive degradation rather than moving into pristine habitats. Techniques to improve the productivity of existing oil palm landscapes should also be employed before expansion is considered. I also suggest buffering these landscapes from adjacent natural forest to reduce any cascading impacts. The effects of hydropower expansion are more difficult to mitigate, as landscapes that would provide high energy outputs often lie within highly pristine forested landscapes and requires extensive areas of inundation. However, efficiency upgrades could be implemented which would help improve energy output from existing hydropower dams without the need for the construction of new dams (Garrett et al., 2021). I also suggest focusing on other potential energy sources such as solar to meet renewable energy targets. My hope is that, given conservation efforts motivated by strong political will, the modification of natural habitat by humans can be limited as we transition to a more sustainable economic model.

Table 6.1. Example papers of species ecological interactions within human altered landscapes. My co-author contribution are highlighted in **bold**.

Species	Authors	Year	Journal	Citation
Asiatic golden cat (*Catopuma temminckii*), Bay cat (*Catopuma badia*)	Decœur, H., Amir, Z., Mendes, C. P., **Moore, J. H.**, & Luskin, M. S.	2023	Biological Conservation	(Decœur et al., 2023)
Common palm civets (*Paradoxurus hermaphroditus*)	Dehaudt, B., Amir, Z., Decoeur, H., Gibson, L., Mendes, C., **Moore, J. H.**, Nursamsi, I., Sovie, A., & Luskin, M. S.	2022	Journal of Animal Ecology	(Dehaudt et al., 2022)
Banded civet (*Hemigalus derbyanus*)	Dunn, A., Amir, Z., Decoeur, H., Dehaudt, B., Nursamsi, I., Mendes, C., **Moore, J. H.**, Negret, P. J., Sovie, A., & Luskin, M. S.	2022	Ecology and Evolution	(Dunn et al., 2022)
Bat spp	Hazard, Q. C. K., Froidevaux, J. S. P., Yoh, N., **Moore, J.**, Senawi, J., Gibson, L., & Palmeirim, A. F.	2023	Biological Conservation	(Hazard et al., 2023)
Marbled cat (*Pardofelis marmorata*)	Hendry, A., Amir, Z., Decoeur, H., Mendes, C. P., **Moore, J. H.**, Sovie, A., & Luskin, M. S.	2023	Ecosphere	(Hendry et al., 2023)
Binturong (*Arctictis binturong*)	Honda, A., Amir, Z., Mendes, C. P., **Moore, J. H.**, & Luskin, M. S.	2023	Oryx	(Honda et al., 2023)
Leopard cats (*Prionailurus bengalensis*)	Luskin, M. S., Arnold, L., Sovie, A., Amir, Z., Chua, M. A. H., Dehaudt, B., Dunn, A., Nursamsi, I., **Moore, J. H.**, & Mendes, C. P.	2023	Wildlife Letters	(Luskin, Arnold, et al., 2023)
Mouse deer (*Tragulus* spp)	Mendes, C. P., Liu, X., Amir, Z., **Moore, J. H.**, & Luskin, M. S.	2023	Austral Ecology	(Mendes et al., 2023)
Sunda pangolin (*Manis javanica*)	Nursamsi, I., Amir, Z., Decoeur, H., **Moore, J. H.**, & Luskin, M. S.	2023	Wildlife Letters	(Nursamsi et al., 2023)

Supplementary materials

Chapter 2: Supplementary materials

Table S2.1. Details of sampling effort per survey period and variables tested.

Year	Isolation	Island	# transects	S	Standardized Abundance	% Rattus	Distance to mainland (m)	NDVI	Area (ha)
1994	6	2	1	0	0	100	426.862	0.306	0.4
1994	6	3	9	1	6	28	1243.251	0.267	1.4
1994	6	5	14	10	3.714	46	907.883	0.35	12.1
1994	6	6	35	11	7.6	38	569.557	0.297	56.3
1994	6	7	2	3	3	80	194.792	0.325	1.9
1994	6	9	12	6	5.25	48	260.457	0.291	10.4
1994	6	16	3	1	0.666	94	503.943	0.257	0.3
1994	6	28	3	1	0.333	97	236.323	0.287	4.7
1994	6	33	3	0	0	100	707.9	0.338	1.7
1994	6	39	3	1	1.333	75	305.093	0.234	1
1994	6	40	3	1	0.333	93	391.915	0.267	0.8
1994	6	41	2	2	2	81	109.911	0.296	1.1
2013	25	2	2	0	0	100	426.862	0.306	0.4
2013	25	3	4	0	0	100	1243.251	0.267	1.4

2013	25	5	8	2	0.25	97	907.883	0.35	12.1
2013	25	6	16	4	0.5	86	569.557	0.297	56.3
2013	25	7	2	1	0.5	95	194.792	0.325	1.9
2013	25	9	6	0	0	100	260.457	0.291	10.4
2013	25	16	2	0	0	100	503.943	0.257	0.3
2013	25	28	4	1	0.75	92	236.323	0.287	4.7
2013	25	33	2	0	0	100	707.9	0.338	1.7
2013	25	39	2	0	0	100	305.093	0.234	1
2013	25	40	2	0	0	100	391.915	0.267	0.8
2013	25	41	2	1	0.5	93	109.911	0.296	1.1
2013	25	X1	10	1	0.1	98	852.049	0.367	23.5
2013	25	X2	4	1	1.75	76	460.251	0.321	10.1
2013	25	X3	9	1	0.111	98	449.484	0.301	24.4
2013	25	X4	10	0	0	100	1606.477	0.307	21.2
2020	33	2	1	0	0	100	426.862	0.306	0.4
2020	33	3	1	0	0	100	1243.251	0.267	1.4
2020	33	5	1	0	0	100	907.883	0.35	12.1
2020	33	6	3	0	0	100	569.557	0.297	56.3
2020	33	7	1	0	0	100	194.792	0.325	1.9
2020	33	9	1	1	3	57	260.457	0.291	10.4
2020	33	28	1	0	0	100	236.323	0.287	4.7

2020	33	38	1	0	0	100	707.9	0.338	1.7
2020	33	39	1	0	0	100	305.093	0.234	1
2020	33	40	1	0	0	100	391.915	0.267	0.8
2020	33	41	1	0	0	100	109.911	0.296	1.1
2020	33	I54	2	0	0	100	380.045	0.341	67.5533
2020	33	I59	1	0	0	100	217.708	0.209	22.4518
2020	33	I63	1	0	0	100	282.966	0.265	7.8719
2020	33	I66	1	0	0	100	337.185	0.27	3.8251
2020	33	I80	1	0	0	100	1243.345	0.331	3.4884
2020	33	I81	1	0	0	100	602.646	0.3	14.9323
2020	33	X1	2	0	0	100	852.049	0.367	23.5
2020	33	X3	2	0	0	100	449.484	0.301	24.4
2020	33	X4	2	1	1.5	63	1606.477	0.307	21.2

“S” represents total number of species, “Standardized abundance” represents standardized abundance to 1 transect per island, “Distance to mainland” represents the distance between the island fragment and the nearest mainland (m), NDVI represents the normalized difference vegetation index, “Area” represents area (ha) of island fragments**.**

Table S2.2. Linear model outputs for species richness and abundance in relation to island size ($\log_{10}$).

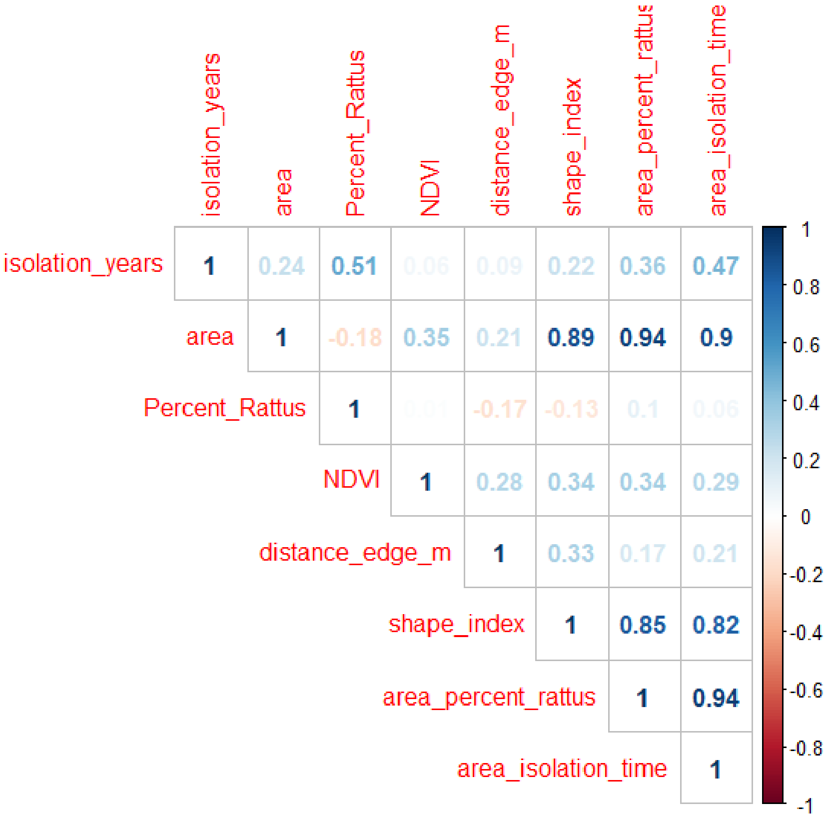
Years	**Metric**	**Intercept**	**$\log_{10}$ Area (ha)**	**SE**	***t* value**	**df**	**R^2**	***P* value**
1992-94	**Richness**	2.325	5.024	0.892	5.630	10	0.73	0.000
2012-13		1.211	0.928	0.317	2.927	14	0.34	0.011
2020		1.022	0.102	0.109	0.941	18	0.05	0.359
1992-94	**Abundance**	6.584	3.921	1.450	2.704	10	0.36	0.022
2012-13		9.258	-1.457	1.569	-0.928	14	0.06	0.369
2020		13.915	-3.597	2.682	-1.341	18	0.04	0.196

Table S2.3. *Rattus* abundance model average results with model importance.

Covariates	**Estimate**	**Std. Error**	**Adjusted SE**	***z* value**	**Importance**
(Intercept)	4.190	0.173	0.176	23.795	NA
$\log_{10}$ Area (ha)	-0.121	0.050	0.051	2.369	1
Isolation years	0.014	0.003	0.003	4.438	1
Distance to mainland (m)	0.000	0.001	0.001	1.235	0.31
NDVI	0.741	0.937	0.963	0.769	0.2

Table S2.4. *Rattus* abundance model selection across all surveys ranked by AIC_C (AIC_C > 4 excluded from table).

			Model parameters							
Years	**Metric**	**Intercept**	**$\log_{10}$ Area (ha)**	**Distance to mainland (m)**	**Isolation Years**	**NDVI**	**df**	**AICc**	**ΔAICc**	**wi**
1994 - 2020	**Abundance**	4.219	-0.121	NA	0.014	NA	4	429.535	0.000	0.352
		4.264	-0.110	0.000	0.014	NA	5	430.508	0.973	0.217
		4.003	-0.135	NA	0.014	0.741	5	431.389	1.854	0.139
		3.954	-0.128	0.000	0.014	1.104	6	431.736	2.202	0.117
		4.264	NA	0.000	0.012	NA	4	432.783	3.248	0.069
		4.200	NA	NA	0.012	NA	3	432.995	3.461	0.062
	Null Model	4.481	NA	NA	NA	NA	2	442.136	12.601	0.001



	isolation_years	area	Percent_Rattus	NDVI	distance_edge_m	shape_index	area_percent_rattus	area_isolation_time
isolation_years	1	0.24	0.51	0.06	0.09	0.22	0.36	0.47
area		1	-0.18	0.35	0.21	0.89	0.94	0.9
Percent_Rattus			1	0.01	-0.17	-0.13	0.1	0.06
NDVI				1	0.28	0.34	0.34	0.29
distance_edge_m					1	0.33	0.17	0.21
shape_index						1	0.85	0.82
area_percent_rattus							1	0.94
area_isolation_time								1

Figure S2.1. Identifying inter-correlations between variables including interaction variables. Shape index and Area * *Rattus* were removed due to autocorrelation.

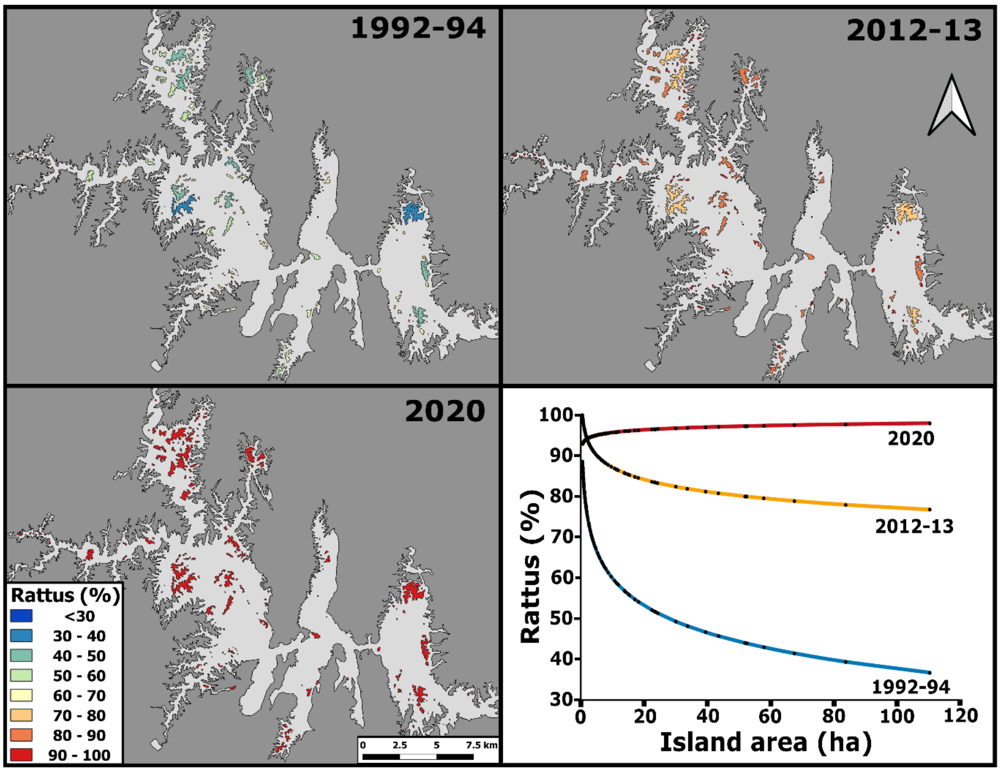


Figure S2.2. Percentage of small mammal captures represented by *R. tiomanicus* in 1992-1994 (t_1), 2012-2013 (t_2), and 2020 (t_3). Final graph shows the relationship between island size and estimated *R. tiomanicus* percentage projected across all islands (labelled as black dots) (see SAR results for model estimates used).

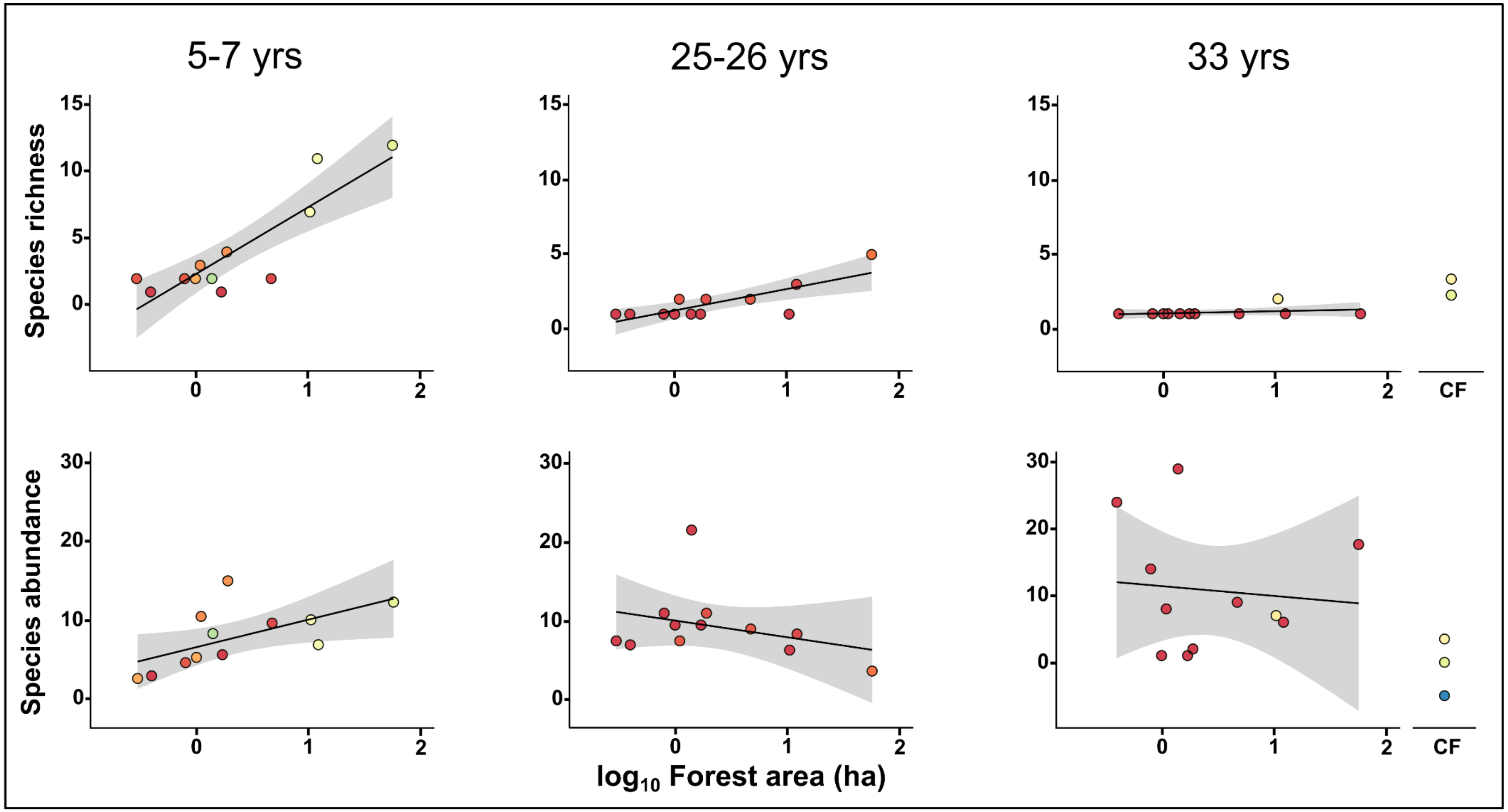
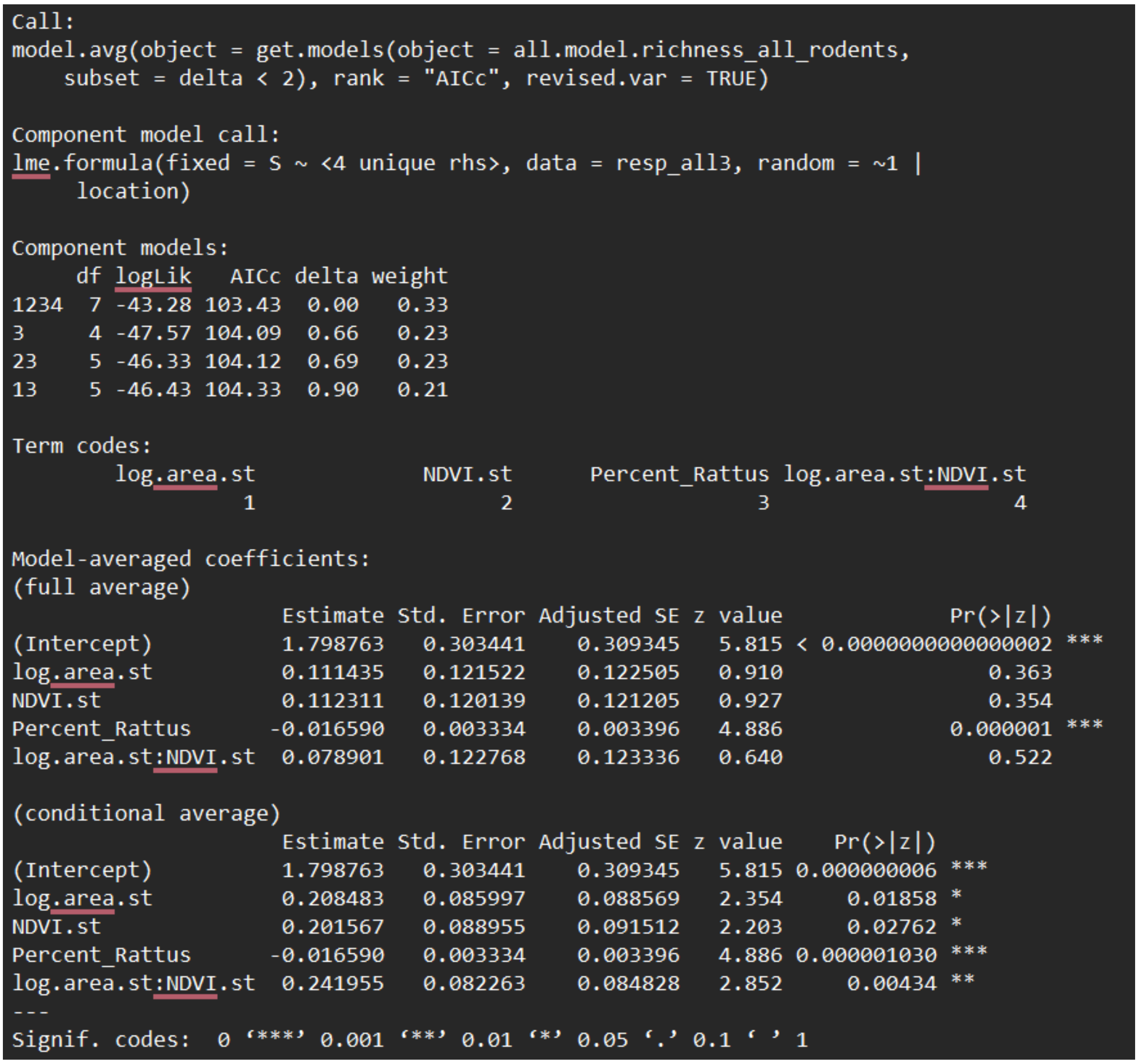


Figure S2.3. Species richness (top) and overall abundance (bottom) vs. island forest area (log$_{10}$) over time, 5-7 years (t_1), 25-26 years (t_2) and 33 years (t_3) post isolation, using only data from the 12 islands resampled during all three time periods. Each circle represents one island fragment. Circles are colour-coded according to the percentage of all individuals represented by *Rattus tiomanicus*. Regression lines (black) with 95% confidence intervals (grey) are highlighted.

Chapter 3: Supplementary materials

ID	Intercept	log.area.st	NDVI.st	Percent_Rattus	log.area.st.NDVI.st	df	logLik	AICc	ΔAICc	weight
16	1.581	0.198	0.183	-0.014	0.241	7	-43.279	103.431	0	0.292
5	2.035	NA	NA	-0.019	NA	4	-47.569	104.091	0.660	0.209
7	1.918	NA	0.226	-0.017	NA	5	-46.328	104.120	0.688	0.206
6	1.739	0.223	NA	-0.016	NA	5	-46.431	104.327	0.895	0.186
8	1.744	0.182	0.233	-0.015	NA	6	-45.721	105.543	2.111	0.101
12	0.431	0.349	0.277	NA	0.354	6	-49.562	113.225	9.794	0.002
2	0.386	0.447	NA	NA	NA	4	-54.097	117.148	13.71	0.000
4	0.468	0.369	0.416	NA	NA	5	-53.425	118.31	14.882	0.000
3	0.491	NA	0.466	NA	NA	4	-57.339	123.630	20.199	0.000
1	0.432	NA	NA	NA	NA	3	-59.984	126.526	23.095	0.000

Table S3.1. Model selection for global model: S ~ log.area.st*NDVI.st + Percent_Rattus , random = ~1|location). Four models highlighted with grey indicating delta <2.



```
Call:
model.avg(object = get.models(object = all.model.richness_all_rodents,
    subset = delta < 2), rank = "AICc", revised.var = TRUE)

Component model call:
lme.formula(fixed = S ~ <4 unique rhs>, data = resp_all3, random = ~1 |
     location)

Component models:
     df logLik   AICc delta weight
1234  7 -43.28 103.43  0.00   0.33
3     4 -47.57 104.09  0.66   0.23
23    5 -46.33 104.12  0.69   0.23
13    5 -46.43 104.33  0.90   0.21

Term codes:
        log.area.st             NDVI.st      Percent_Rattus log.area.st:NDVI.st
                  1                   2                   3                   4

Model-averaged coefficients:
(full average)
                     Estimate Std. Error Adjusted SE z value             Pr(>|z|)
(Intercept)          1.798763   0.303441    0.309345   5.815 < 0.0000000000000002 ***
log.area.st          0.111435   0.121522    0.122505   0.910                0.363
NDVI.st              0.112311   0.120139    0.121205   0.927                0.354
Percent_Rattus      -0.016590   0.003334    0.003396   4.886             0.000001 ***
log.area.st:NDVI.st  0.078901   0.122768    0.123336   0.640                0.522

(conditional average)
                     Estimate Std. Error Adjusted SE z value    Pr(>|z|)
(Intercept)          1.798763   0.303441    0.309345   5.815 0.000000006 ***
log.area.st          0.208483   0.085997    0.088569   2.354     0.01858 *
NDVI.st              0.201567   0.088955    0.091512   2.203     0.02762 *
Percent_Rattus      -0.016590   0.003334    0.003396   4.886 0.000001030 ***
log.area.st:NDVI.st  0.241955   0.082263    0.084828   2.852     0.00434 **
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

Figure S3.1. Model averaging results for small mammal predictor variables. With full average and conditional average results.

Table S3.2. Sum of weights for the model selection of predictor variables impacting native species richness.

	Percent_Rattus	NDVI.st	log.area.st	log.area.st:NDVI.st
Sum of weights	1	0.56	0.53	0.33
N containing models	4	2	2	1

Chapter 5: Supplementary materials

New camera trapping for within-site abundance analyses

We assessed pig and macaque abundance in ten lowland primary rainforest landscapes in Thailand (two sites), Peninsular Malaysia (two sites), Singapore (one site), Sumatra (three sites), and Borneo (two sites; Figure 5.2A). In Sumatra, Indonesia, we surveyed Gunung Leuser National Park (8,630 km^2), Kerinci Seblat National Park (13,753 km^2), and Bukit Barisan Selatan National Park (3,568 km^2), which together comprise the UNESCO Tropical Rainforest Heritage of Sumatra (Luskin, Brashares, et al., 2017). At each site, we additionally surveyed forest fragments adjacent to each national park. In Malaysian Borneo, I surveyed one large, fragmented site in Sawarak, Malaysian Borneo (Lambir Hills National Park, 69.5 km^2) that has experienced substantial historical hunting pressures (Harrison et al., 2013) and one intact site in Sabah, Malaysian Borneo [Danum Valley Conservation Area (DVCA), 438 km^2] that is not hunted. In Singapore, we surveyed the Central Catchment Nature Reserve (CCNR, 37 km^2), Sentosa and Southern ridges (~1 km^2 each), and the offshore island Pulau Ubin (10 km^2). In Peninsular Malaysia, I surveyed Pasoh Forest Reserve (PFR, 130 km^2), which is connected to other forests but bordered on three sides by oil palm plantations (Luskin, Brashares, et al., 2017), as well as Ulu Muda Forest (1,600 km^2), which contains one of the largest extents of lowland primary forest outside of a protected area in Peninsular Malaysia. In southern Thailand we surveyed Khao Ban Tat Wildlife Sanctuary (1,267 km^2), which is a fragmented sliver of forest along a low mountain range that is the continental divide, and Khao Yai National Park in central Thailand, which has a 2,168 km^2 intact forest area and is connected to the larger UNESCO World Heritage Dong Phayayen-Khao Yai Forest Complex.

We collected information on pigs and macaques using systematic landscape-scale camera trapping. At each site we deployed 22–112 passive infrared cameras traps set across areas of 8–814 km^2 (Table S5.6). Cameras were placed within a pre-mapped grid and spaced 500–2000 m apart in large forests (>20 km^2) and 100–500 m apart in smaller forest fragments and on islands (e.g. Pulau Ubin). We standardized deployment methods among sites by attaching passive camera traps to trees at 0.2–0.3 m height along hiking trails or natural wildlife trails and without baits. Cameras were deployed for 60–90 days at each site from December 2013 until March 2019 and we considered captures independent if they were at least 30 minutes apart.

Within-site abundance analyses using N-mixture models

We estimated abundance for each species using single-species N-mixture models that account for imperfect detection (Royle, 2004). Hierarchical abundance modelling is a linked two-step process wherein the observational variable (number of individuals detected during consecutive sampling periods) informs detection probability, and the second step estimates true abundance across the landscape. Detection-corrected estimates for abundance provide a relatively unbiased metric compared to traditional camera trap measures such as relative abundance indices and naïve occupancy, and are closely correlated with true abundance (MacKenzie & Nichols, 2004). We resampled all camera trap locations into 0.86 km^2 hexagonal grid cells to be used as sampling units within the detection history matrix in order to ensure sampling units were spatially independent to satisfy the population closure assumptions in the model (Figure S5.3). Moreover, due to the 60–90 day deployment time of cameras per survey, it is assumed that individual surveys are temporally closed to population change, further satisfying the model's population closure assumption. For each species, we produced detection history matrices denoting the number of individuals detected in a sampling occasion, a zero if the species was not detected, and no data if the sampling occasion or sampling unit were not active. We used sampling occasions of 3 days to reduce zero-inflation. The matrices containing the single-species N-mixture models were run with data from all surveys, and the survey identifier was included as a blocking factor covariate to allow the estimation of differing abundance for each survey. The only variable included to affect detection probability was the total effort per sampling unit, which helps account for different effort among camera traps within a sampling unit. To examine how environmental variables affected species abundance, we included these as covariates in the N-mixture models. Continuous covariates were standardized using the function *decostand()* in the R package *vegan* (Oksanen et al., 2016) before being included in the models, which substantially improved model performance. For each camera, we generated values for each covariate within 250, 500, 1,000, 5,000, and 10,000 m buffer zones (see Table S5.4 for a full list of covariates) and when spatially resampling cameras into hexagonal grid cells, we took the average covariate value from the cameras included. All N-mixture modelling with environmental covariates was implemented using the function *pcount()* in the R package *unmarked* (Fiske & Chandler, 2011). Covariates that were found to have a significant effect on pig and macaque abundance were those that had a P-value of < 0.05 in the N-mixture model. After N-mixture models were constructed, the *predict()* function was used to back-transform estimated abundance in response to the relevant landscape covariates. To visualize the relationship between pigs and macaques as a function of specific landscape covariates, the relationship was plotted in R with the *ggplot2* package.

Table S5.1. Literature review of density estimates for long-tailed macaque, pig-tailed macaque and wild boar with corresponding Forest Landscape Integrity Index (FLII) value.

Source	Region	Country	Landscape	Year of data	Density	FLII	Species	Latitude	Longitude
(Ahrestani, 1999)	S_Asia	India	Bhadra Wildlife Sancutary	1998	2	8.53	Wild boar	13.60773	75.65375
(Anggraeni et al., 2013)	SE_Asia	Indonesia	Surabaya	2012	55	2.42	Long-tailed macaque	–7.31773	112.8393
(Avinandan et al., 2008)	S_Asia	India	Sariska Tiger Reserve, Rajasthan	2002	17.52	5.72	Wild boar	27.31049	76.43898
(Bhattarai & Kindlmann, 2013)	S_Asia	Nepal	Chitwan National Park, Narayani	2010	6.36	6.20	Wild boar	27.551	84.471
(Biswas & Sankar, 2002)	S_Asia	India	Pench National Park, Madhya Pradesh	1998	2.59	7.95	Wild boar	21.81303	79.3555
(Brotcorne, 2014)	SE_Asia	Indonesia	Bali	2014	70	5.25	Long-tailed macaque	–8.16105	114.4785
(Caldecott, 1983)	SE_Asia	Malaysia	Lima Belas Esates	1983	27.5	1.14	Pig-tailed macaque	3.794768	101.3523
(Dinerstein, 1989)	S_Asia	Nepal	Royal Karnali-Bardia Wildlife Reserve	1978	4	8.55	Wild boar	28.583	81.333
(Eisenberg & Lockhart, 1972)	S_Asia	Sri Lanka	Wilpattu National Park	1970	0.75	8.24	Wild boar	8.457385	80.04866
(Fauzi et al., 2020)	SE_Asia	Indonesia	Kelimutu National Park	2010	5	7.56	Long-tailed macaque	–8.77754	121.7842
(Gopalaswamy et al., 2012)	S_Asia	India	Bhadra Tiger Reserve	2012	2.46	8.17	Wild boar	13.509	75.631
(J. Gray, 2009)	S_Asia	Nepal	Bardia National Park, Bardia	1996	2.8	8.47	Wild boar	28.35746	81.56186

(T. N. E. Gray et al., 2012)	SE_Asia	Cambodia	Mondulkiri Protected Forest CORE	2008	1.9	9.58	Wild boar	12.85872	107.3963
(T. N. E. Gray et al., 2012)	SE_Asia	Cambodia	PhNom Prich Wildlife Sanctuary	2008	1.4	9.44	Wild boar	12.76143	106.8649
(T. N. E. Gray et al., 2012)	SE_Asia	Cambodia	Mondulkiri Protected Forest Edge	2008	1.9	8.20	Wild boar	12.7612	107.3715
(Afendi et al., 2011)	SE_Asia	Indonesia	Karimunjawa	2008	11.46	4.61	Long-tailed macaque	–5.85003	110.4406
(M. F. Hansen et al., 2019)	SE_Asia	Indonesia	Baluran National Park	2019	41.1	6.93	Long-tailed macaque	–7.85261	114.4055
(Haque, 1990)	S_Asia	India	Keoladeo Ghana Sanctuary	1988	2.24	0.00	Wild boar	27.15574	77.52404
(Harihar et al., 2009)	S_Asia	India	Rajaji National Park	2005	1.1	6.96	Wild boar	29.93525	78.31822
(Harihar et al., 2009)	S_Asia	India	Rajaji National Park	2006	1.9	6.87	Wild boar	29.99102	78.29019
(Harihar et al., 2009)	S_Asia	India	Rajaji National Park	2004	8.1	6.87	Wild boar	29.99102	78.29019
(Harihar et al., 2011)	S_Asia	India	Ranthambhore National Park	2006	3.5	6.87	Wild boar	29.99102	78.29019
(Ickes et al., 2001)	SE_Asia	Peninsular Malaysia	Pasoh Research Forest	1998	27	3.80	Wild boar	2.983	102.21
(Ickes et al., 2001)	SE_Asia	Peninsular Malaysia	Pasoh Research Forest	1996	47	3.80	Wild boar	2.983	102.21
(Inayatullah, 1973)	S_Asia	Pakistan	Changa Manga Forest	1970	10.4	0.00	Wild boar	31.08765	73.97503
(Johnsingh, 1983)	S_Asia	India	Bandipur Tiger Reserve	1980	2.5	9.14	Wild boar	11.77887	76.46463
(Kamler et al., 2012)	SE_Asia	Laos	Nam Et-Phou Louey (NEPL)	2010	3.19	7.95	Wild boar	20.43773	103.6066

(Kapfer et al., 2011)	S_Asia	Nepal	Chitwan National Park, Narayani	1991	2	7.36	Wild boar	27.47134	84.52246
(Karanth & Nichols, 1998)	S_Asia	India	Kanha National Park	1995	2.5	8.97	Wild boar	22.33768	80.61165
(Karanth & Nichols, 1998)	S_Asia	India	Pench National Park, Madhya Pradesh	1995	0.8	8.54	Wild boar	21.64513	79.24729
(Karanth & Nichols, 1998)	S_Asia	India	Nagarahole National Park	1996	3.3	8.09	Wild boar	12.03222	76.12099
(Karanth & Nichols, 1998)	S_Asia	India	Kaziranga Wildlife Sanctuary	1996	2.6	6.59	Wild boar	26.58652	93.17946
(Karanth & Sunquist, 1992)	S_Asia	India	Nagarahole National Park	1988	1.2	8.09	Wild boar	12.03222	76.12099
(Karanth & Sunquist, 1992)	S_Asia	India	Nagarahole National Park	1988	10.1	8.08	Wild boar	12.03536	76.11832
(Karanth & Sunquist, 1992)	S_Asia	India	Nagarahole National Park	1992	4.2	8.05	Wild boar	12.025	76.108
(Karanth et al., 2004)	S_Asia	India	Tadoba Andheri Tiger Reserve	2002	2.63	9.41	Wild boar	20.24837	79.36066
(Karanth et al., 2004)	S_Asia	India	Melghat Tiger Reserve	2003	0.5	9.05	Wild boar	21.40608	77.14844
(Karanth et al., 2004)	S_Asia	India	Kanha National Park	1996	1.9	8.97	Wild boar	22.33768	80.61165
(Karanth et al., 2004)	S_Asia	India	Bandipur Tiger Reserve	1999	0.65	9.15	Wild boar	11.78504	76.46449
(Karanth et al., 2004)	S_Asia	India	Pench National Park (MH)	2003	2.03	8.54	Wild boar	21.64513	79.24729
(Karanth et al., 2004)	S_Asia	India	Nagarahole National Park	1996	3.4	8.09	Wild boar	12.03222	76.12099

(Karanth et al., 2004)	S_Asia	India	Bhadra Wildlife Sancutary	1998	2.7	8.21	Wild boar	13.69492	75.63531
(Karanth et al., 2004)	S_Asia	India	Panna National Park	2001	1.93	5.95	Wild boar	24.59029	79.94441
(Karki, 2011)	S_Asia	Nepal	Bardia National Park, Bardia	2008	4	8.55	Wild boar	28.583	81.333
(Karki, 2011)	S_Asia	Nepal	Gir Forest, Gujarat	2008	4.2	6.20	Wild boar	27.551	84.471
(Kawanishi & Sunquist, 2004)	SE_Asia	Peninsular Malaysia	Taman Negara (Kuala Terengan)	2000	3.63	8.77	Wild boar	4.533	102.429
(Kawanishi & Sunquist, 2004)	SE_Asia	Peninsular Malaysia	Taman Negara (Merapoh)	2000	4.17	8.05	Wild boar	4.623	102.068
(Kawanishi & Sunquist, 2004)	SE_Asia	Peninsular Malaysia	Taman Negara (Kuala Koh)	2000	4.62	7.92	Wild boar	4.847	102.45
(Krishnakumar et al., 2020)	S_Asia	India	Mundanthurai Tiger Reserve	2016	8.8	8.81	Wild boar	8.690662	77.31162
(Kumaraguru et al., 2011)	S_Asia	India	Anamalai Tiger Reserve	2004	20.6	7.16	Wild boar	10.17875	77.17723
(Lovari et al., 2015)	S_Asia	Nepal	Suklaphanta Wildlife Reserve, Terai Nepal	2011	1.8	6.51	Wild boar	28.87409	80.27745
(Majumder et al., 2011)	S_Asia	India	Pench National Park, Madhya Pradesh	2008	4	7.79	Wild boar	21.83308	79.43389
(Majumder et al., 2011)	S_Asia	India	Pench National Park, Madhya Pradesh	2009	5.7	7.79	Wild boar	21.83308	79.43389
(Majumder et al., 2011)	S_Asia	India	Pench National Park, Madhya Pradesh	2010	9.35	7.79	Wild boar	21.83308	79.43389

(Majumder et al., 2011)	S_Asia	India	Pench National Park, Madhya Pradesh	2007	10.2	7.79	Wild boar	21.83308	79.43389
(McConkey & Chivers, 2004)	SE_Asia	Indonesia	Barito Ulu, Central Kalimantan	1996	0.2	8.91	Pig-tailed macaque	0	114
(McKay, 1973)	S_Asia	Sri Lanka	Gal Oya National Park	1970	0.6	7.85	Wild boar	7.228476	81.47179
(Mondal et al., 2011)	S_Asia	India	Sariska Tiger Reserve, Rajasthan	2008	54	5.73	Wild boar	27.31049	76.43898
(O'Kelly & Nut, 2010)	SE_Asia	Cambodia	Seima Protected Forest	2008	2.04	7.91	Wild boar	12.27392	106.9509
(O'Brien et al., 2003)	SE_Asia	Indonesia - Sumatra	Bukit Barisan Selatan National Park on Sumatra	1999	4.4	6.64	Wild boar	–5.65889	104.4058
(O'Brien et al., 2003)	SE_Asia	Indonesia - Sumatra	Bukit Barisan Selatan National Park on Sumatra	1999	4.6	6.64	Wild boar	–5.65889	104.4058
(O'Brien et al., 2003)	SE_Asia	Indonesia - Sumatra	Bukit Barisan Selatan National Park on Sumatra	1998	6.06	6.64	Wild boar	–5.65889	104.4058
(Oi, 1990)	SE_Asia	Indonesia	West Sumatra	1986	53	5.68	Pig-tailed macaque	–1.6	101.26
(Ramesh et al., 2009)	S_Asia	India	Mudumalai Tiger Reserve	2008	1.3	8.59	Wild boar	11.5622	76.53458
(Reza et al., 2002)	S_Asia	India	Katka-Kochikhali in the Sundarbans	2000	1.95	9.93	Wild boar	21.96975	89.61087
(Reza et al., 2002)	S_Asia	India	Katka-Kochikhali in the Sundarbans	2000	2.2	9.93	Wild boar	21.96975	89.61087

(Reza et al., 2002)	S_Asia	India	Katka-Kochikhali in the Sundarbans	2000	2.3	9.93	Wild boar	21.96975	89.61087
(Reza et al., 2002)	S_Asia	India	Katka-Kochikhali in the Sundarbans	2000	15.8	7.93	Wild boar	22.26773	89.20178
(Rijksen, 1978)	SE_Asia	Indonesia	KETAMBE	1975	19	7.83	Pig-tailed macaque	3.683333	97.65
(Riley et al., 2015)	SE_Asia	Singapore	Singapore_CCNR	2012	30.19	0.60	Long-tailed macaque	1.355369	103.7799
(Riley et al., 2015)	SE_Asia	Singapore	Singapore_CCNR	2012	24.45	0.78	Long-tailed macaque	1.33882	103.8275
(Riley et al., 2015)	SE_Asia	Singapore	Singapore_CCNR	2012	33.63	0.51	Long-tailed macaque	1.406222	103.7861
(Riley et al., 2015)	SE_Asia	Singapore	Singapore_CCNR	2012	12.57	0.66	Long-tailed macaque	1.379442	103.8284
(Riley et al., 2015)	SE_Asia	Singapore	Singapore_Islands	2012	4.21	1.56	Long-tailed macaque	1.406222	104.0612
(Rostro-García et al., 2018)	SE_Asia	Cambodia	Srepok Wildlife Sanctuary	2014	6.5	9.70	Wild boar	12.93618	107.3051
(Muhd Sahimi et al., 2020)	SE_Asia	Indonesia	Gunung Basur Permanent Forest Reserve	2019	0.02	7.53	Pig-tailed macaque	5.468691	101.797
(Sankar et al., 2010)	S_Asia	India	Sariska Tiger Reserve, Rajasthan	2008	15.4	5.73	Wild boar	27.31049	76.43898
(Santiapillai et al., 1982)	S_Asia	Sri Lanka	Ruhuna National Park (part of Yala)	1978	0.7	8.02	Wild boar	6.643761	81.35242
(Schaller, 1967)	S_Asia	India	Kanha National Park	1965	1.2	8.97	Wild boar	22.33768	80.61165
(Seidensticker, 1976)	S_Asia	Nepal	Royal Chiwan National Park	1975	5.8	6.20	Wild boar	27.551	84.471
(Muthamizh Selvan et al., 2014)	S_Asia	India	Pakke Tiger Reserve, Pradesh	2009	4.1	8.00	Wild boar	27.00429	92.7813

(Muthamizh Selvan et al., 2014)	S_Asia	India	Pakke Tiger Reserve, Pradesh	2010	6.6	8.00	Wild boar	27.00429	92.7813
(Muthamizh Selvan et al., 2014)	S_Asia	India	Pakke Tiger Reserve, Pradesh	2011	9.3	8.00	Wild boar	27.00429	92.7813
(Sha & Hanya, 2013)	SE_Asia	Singapore	Singapore_CCNR	2012	47.6	0.60	Long-tailed macaque	1.355369	103.7799
(Sha et al., 2009)	SE_Asia	Singapore	Singapore_CCNR	2007	28.2	0.60	Long-tailed macaque	1.355369	103.7799
(Spillett, 1967c)	S_Asia	India	Keoladeo Ghana Sanctuary	1965	2.9	0.00	Wild boar	27.15574	77.52404
(Spillett, 1967a)	S_Asia	India	Jaldapara Wildlife Sanctuary	1965	1.3	3.90	Wild boar	26.68644	89.29397
(Spillett, 1967b)	S_Asia	India	Kaziranga Wildlife Sanctuary	1965	1.4	6.59	Wild boar	26.58652	93.17946
(Srikosamatara, 1993)	SE_Asia	Thailand	Huai Kha Khaeng Wildlife Santcuary	1990	1.6	9.60	Wild boar	15.46793	99.29478
(Srivastava & Khan, 2009)	S_Asia	India	Keoladeo National Park, Bharatpur	2007	15.7	0.00	Wild boar	27.18562	77.51252
(Vongkhamheng et al., 2013)	SE_Asia	Laos	Nam Et-Phou Louey National Park	2008	3.19	7.87	Wild boar	20.46088	103.6377
(S. W. Wang, 2010)	S_Asia	Bhutan	Jigme Singye Wangchuck National Park	2008	3.7	8.08	Wild boar	21.63333	79.00222
(Wegge et al., 2009)	S_Asia	Nepal	Royal Karnali-Bardia Wildlife Reserve	2007	2.2	8.47	Wild boar	28.35746	81.56186
(Wegge et al., 2009)	S_Asia	Nepal	Royal Karnali-Bardia Wildlife Reserve	1997	2.2	8.47	Wild boar	28.35746	81.56186

(Wegge et al., 2009)	S_Asia	Nepal	Royal Karnali-Bardia Wildlife Reserve	2007	3.5	8.55	Wild boar	28.583	81.333
(Wegge et al., 2009)	S_Asia	Nepal	Royal Karnali-Bardia Wildlife Reserve	2007	8.22	7.76	Wild boar	28.2796	81.47948
(Yanuar et al., 2009)	SE_Asia	Indonesia	Kerinci Seblat National Park - Lowland	1998	14.7	5.92	Pig-tailed macaque	–3.03083	101.7935
(Yanuar et al., 2009)	SE_Asia	Indonesia	Kerinci Seblat National Park - Hill	1998	15.7	6.37	Pig-tailed macaque	–3.07679	102.1194
(Yanuar et al., 2009)	SE_Asia	Indonesia	Kerinci Seblat National Park - Sub-Montane	1998	5.9	9.34	Pig-tailed macaque	–2.7585	102.0675
(Yanuar et al., 2009)	SE_Asia	Indonesia	Kerinci Seblat National Park - Montane	1998	4.8	8.24	Pig-tailed macaque	–1.49983	100.8693
(Yanuar et al., 2009)	SE_Asia	Indonesia	Kerinci Seblat National Park - Lowland	1998	10.7	5.92	Long-tailed macaque	–3.03083	101.7935
(Yanuar et al., 2009)	SE_Asia	Indonesia	Kerinci Seblat National Park - Hill	1998	6.6	6.37	Long-tailed macaque	–3.07679	102.1194

Table S5.2. Capture rates of long-tailed macaque, pig-tailed macaque, wild boar and bearded pig with corresponding data sources and oil palm landscape values. RAI, relative abundance index. Oil palm group was classified as high where oil palm represented >20% of land cover, and low where it represented <1%.

Source	Trapping effort (camera nights)	Landscape	Species	Records	RAI	Oil palm group	% Oil palm 20km	Latitude	Longitude
(T. N. E. Gray & Channa, 2011)	2717	Phnom Prich WS	Wild boar	155	5.70	Low	0.00	12.801	106.501
(T. N. E. Gray & Channa, 2011)	2717	Phnom Prich WS	Long-tailed macaque	2	0.07	Low	0.00	12.801	106.501
(Clements, 2013)	25904	Perak	Long-tailed macaque	169	0.65	Low	0.7608912	5.5	101
(Clements, 2013)	25904	Perak	Bearded pig	0	0.00	Low	0.76	5.5	101
(Clements, 2013)	25904	Perak	Wild boar	4168	16.09	Low	0.76	5.5	101
(Clements, 2013)	25904	Perak	Pig-tailed macaque	402	1.55	Low	0.76	5.5	101
(Cheyne & Macdonald, 2011)	22588	Sabangau	Pig-tailed macaque	512	2.27	Low	0.00	– 2.333162	113.89172
(Cheyne & Macdonald, 2011)	22588	Sabangau	Long-tailed macaque	4	0.02	Low	0.00	–2.333162	113.89172

(Cheyne & Macdonald, 2011)	22588	Sabangau	Bearded pig	147	0.65	Low	0.00	–2.333162	113.89172
(Yue et al., 2015)	1299	Ulu Segama	Long-tailed macaque	1	0.08	High	26.02	4.768259	117.86526
(Yue et al., 2015)	1299	Ulu Segama	Pig-tailed macaque	47	3.62	High	26.02	4.768259	117.86526
(Yue et al., 2015)	1299	Ulu Segama	Bearded pig	132	10.16	High	26.02	4.768259	117.86526
(Sunarto, 2011)	7513	Riau Province	Pig-tailed macaque	607	8.08	Low	0.51	–0.921494	102.38577
(Sunarto, 2011)	7513	Riau Province	Bearded pig	27	0.36	Low	0.51	–0.921494	102.38577
(Sunarto, 2011)	7513	Riau Province	Wild boar	112	1.49	Low	0.51	–0.921494	102.38577
(Sunarto, 2011)	7513	Riau Province	Long-tailed macaque	10	0.13	Low	0.51	–0.921494	102.38577
(O’Brien et al., 2003)	9095	Bukit Barisan Selatan	Long-tailed macaque	2	0.02	Low	0.23	–5.769092	104.53717
(O’Brien et al., 2003)	9095	Bukit Barisan Selatan	Pig-tailed macaque	169	1.86	Low	0.23	–5.769092	104.53717
(O’Brien et al., 2003)	9095	Bukit Barisan Selatan	Wild boar	162	1.78	Low	0.23	–5.769092	104.53717
(O’Brien et al., 2003)	3030	Bukit Barisan Selatan	Long-tailed macaque	0	0.00	Low	0.00	–4.892919	103.80935
O'Brien *et al.* (2003)	3030	Bukit Barisan Selatan	Pig-tailed macaque	102	3.37	Low	0.00	–4.892919	103.80935

(O’Brien et al., 2003)	3030	Bukit Barisan Selatan	Wild boar	96	3.17	Low	0.00	–4.892919	103.80935
O'Brien *et al.* (2003)	8409	Bukit Barisan Selatan	Long-tailed macaque	1	0.01	Low	0.78	–5.326913	104.19866
(O’Brien et al., 2003)	8409	Bukit Barisan Selatan	Pig-tailed macaque	171	2.03	Low	0.78	–5.326913	104.19866
(O’Brien et al., 2003)	8409	Bukit Barisan Selatan	Wild boar	119	1.42	Low	0.78	–5.326913	104.19866
(Haidir et al., 2018)	8399	Kerinci Seblat	Wild boar	39	0.46	Low	0.00	–1.870837	101.88721
(Haidir et al., 2018)	8399	Kerinci Seblat	Pig-tailed macaque	413	4.92	Low	0.00	–1.870837	101.88721
(Haidir et al., 2018)	8399	Kerinci Seblat	Bearded pig	0	0.00	Low	0.00	–1.870837	101.88721
(Haidir et al., 2018)	8399	Kerinci Seblat	Long-tailed macaque	0	0.00	Low	0.00	–1.870837	101.88721
(Haidir et al., 2018)	7053	Kerinci Seblat	Wild boar	32	0.45	Low	0.00	–2.264451	101.79425
(Haidir et al., 2018)	7053	Kerinci Seblat	Bearded pig	1	0.01	Low	0.00	–2.264451	101.79425
(Haidir et al., 2018)	7053	Kerinci Seblat	Pig-tailed macaque	606	8.59	Low	0.00	–2.264451	101.79425
(Haidir et al., 2018)	7053	Kerinci Seblat	Long-tailed macaque	0	0.00	Low	0.00	–2.264451	101.79425
(Beaudrot et al., 2019)	522	Nam Kading	Wild boar	13	2.49	Low	0.00	18.316667	104.01
(Beaudrot et al., 2019)	817	Nam Kading	Wild boar	34	4.16	Low	0.00	18.316667	104.01
(Beaudrot et al., 2019)	679	Nam Kading	Wild boar	25	3.68	Low	0.00	18.316667	104.01

(Beaudrot et al., 2019)	792	Nam Kading	Wild boar	50	6.31	Low	0.00	18.316667	104.01
(Beaudrot et al., 2019)	768	Nam Kading	Wild boar	27	3.52	Low	0.00	18.316667	104.01
(Beaudrot et al., 2019)	766	Nam Kading	Wild boar	38	4.96	Low	0.00	18.316667	104.01
(Grassman et al., 2006)	1224	Phu Khieo WS	Wild boar	40	3.27	Low	0.00	16.401	101.401
(Grassman et al., 2006)	1224	Phu Khieo WS	Long-tailed macaque	0	0.00	Low	0.00	16.401	101.401
(Srikosamatara, 1993)	1000	Huai Kha Khaeng WS	Long-tailed macaque	0	0.00	Low	0.00	15.708765	99.420847
(Srikosamatara, 1993)	1000	Huai Kha Khaeng WS	Wild boar	2	0.20	Low	0.00	15.708765	99.420847
(Van Schaik & Griffiths, 1996)	2000	Gunung Leuser	Long-tailed macaque	0	0.00	Low	0.08	3.2010056	97.403428
(Van Schaik & Griffiths, 1996)	2000	Gunung Leuser	Pig-tailed macaque	7	0.35	Low	0.08	3.2010056	97.403428
(Van Schaik & Griffiths, 1996)	2000	Gunung Leuser	Wild boar	24	1.20	Low	0.08	3.2010056	97.403428
(Van Schaik & Griffiths, 1996)	1000	Ujung Kulon NP	Long-tailed macaque	0	0.00	Low	0.00	–6.666667	105.33333
(Van Schaik & Griffiths, 1996)	1000	Ujung Kulon NP	Wild boar	302	30.20	Low	0.00	–6.666667	105.33333
(Kawanishi & Sunquist, 2004)	4847	Taman Negara	Pig-tailed macaque	3	0.06	Low	0.50	4.388255	102.39729

(Kawanishi & Sunquist, 2004)	4847	Taman Negara	Long-tailed macaque	0	0.00	Low	0.50	4.388255	102.39729
(Kawanishi & Sunquist, 2004)	4847	Taman Negara	Wild boar	117	2.41	Low	0.50	4.388255	102.39729
(Kawanishi & Sunquist, 2004)	4847	Taman Negara	Bearded pig	0	0.00	Low	0.50	4.388255	102.39729
(Novarino, 2005)	2720	Taratak Sungai Lundang	Long-tailed macaque	22	0.81	Low	0.00	–1.043164	100.54006
(Novarino, 2005)	2720	Taratak Sungai Lundang	Pig-tailed macaque	119	4.38	Low	0.00	–1.043164	100.54006
(Novarino, 2005)	2720	Taratak Sungai Lundang	Bearded pig	0	0.00	Low	0.00	–1.043164	100.54006
(Novarino, 2005)	2720	Taratak Sungai Lundang	Wild boar	29	1.07	Low	0.00	–1.043164	100.54006
(Maddox et al., 2007)	7102	PT Asiatic Persada	Long-tailed macaque	67	0.94	High	41.17	–1.91525	103.34634
(Maddox et al., 2007)	7102	PT Asiatic Persada	Pig-tailed macaque	855	12.04	High	41.17	–1.91525	103.34634
(Maddox et al., 2007)	7102	PT Asiatic Persada	Bearded pig	442	6.22	High	41.17	–1.91525	103.34634
(Maddox et al., 2007)	7102	PT Asiatic Persada	Wild boar	1861	26.20	High	41.17	–1.91525	103.34634
(Lynam et al., 2007)	785	Temenggor	Wild boar	16	2.04	Low	0.00	5.491777	101.58395

(Lynam et al., 2007)	785	Temenggor	Long-tailed macaque	0	0.00	Low	0.00	5.491777	101.58395
(Lynam et al., 2007)	785	Temenggor	Pig-tailed macaque	13	1.66	Low	0.00	5.491777	101.58395
(Lynam et al., 2007)	785	Temenggor	Bearded pig	0	0.00	Low	0.00	5.491777	101.58395
(Lynam et al., 2007)	495	Cameron Highlands	Wild boar	6	1.21	Low	0.00	4.571533	101.40466
(Lynam et al., 2007)	495	Cameron Highlands	Pig-tailed macaque	2	0.40	Low	0.00	4.571533	101.40466
(Lynam et al., 2007)	495	Cameron Highlands	Bearded pig	0	0.00	Low	0.00	4.571533	101.40466
(Lynam et al., 2007)	768	Taman Negara	Bearded pig	0	0.00	Low	0.00	4.67491	102.56766
(Lynam et al., 2007)	768	Taman Negara	Pig-tailed macaque	1	0.13	Low	0.00	4.67491	102.56766
(Lynam et al., 2007)	768	Taman Negara	Wild boar	10	1.30	Low	0.00	4.67491	102.56766
(Lynam et al., 2007)	768	Taman Negara	Long-tailed macaque	0	0.00	Low	0.00	4.67491	102.56766
(Lynam et al., 2007)	1172	Pekan	Wild boar	11	0.94	High	32.38	3.596469	103.09533
(Lynam et al., 2007)	1172	Pekan	Bearded pig	0	0.00	High	32.38	3.596469	103.09533
(Lynam et al., 2007)	1172	Pekan	Pig-tailed macaque	11	0.94	High	32.38	3.596469	103.09533
(Lynam et al., 2007)	1172	Pekan	Long-tailed macaque	1	0.09	High	32.38	3.596469	103.09533

(McShea et al., 2009)	5679	Bintulu acacia	Long-tailed macaque	2	0.04	High	33.68	3.3253287	113.26786
(McShea et al., 2009)	5679	Bintulu acacia	Pig-tailed macaque	105	1.85	High	33.68	3.3253287	113.26786
(McShea et al., 2009)	5679	Bintulu acacia	Bearded pig	68	1.20	High	33.68	3.3253287	113.26786
(McShea et al., 2009)	7295	Phnom Prich WS	Long-tailed macaque	0	0.00	Low	0.00	12.936181	107.30507
(McShea et al., 2009)	7295	Phnom Prich WS	Wild boar	330	4.52	Low	0.00	12.936181	107.30507
(Jenks et al., 2011)	6260	Khao Yai NP	Long-tailed macaque	0	0.00	Low	0.00	14.441389	101.36972
(Jenks et al., 2011)	6260	Khao Yai NP	Wild boar	60	0.96	Low	0.00	14.441389	101.36972
(Linkie, 2006)	2000	Kerinci Seblat	Bearded pig	22	1.10	Low	0.00	–2.416667	101.48333
(Linkie, 2006)	2000	Kerinci Seblat	Long-tailed macaque	0	0.00	Low	0.00	–2.416667	101.48333
(Linkie, 2006)	2000	Kerinci Seblat	Pig-tailed macaque	134	6.70	Low	0.00	–2.416667	101.48333
(Linkie, 2006)	2000	Kerinci Seblat	Wild boar	6	0.30	Low	0.00	–2.416667	101.48333
(Wibisono et al., 2009)	1728	Batang Gadis NP	Long-tailed macaque	5	0.29	Low	0.00	0.983333	99.383333
(Wibisono et al., 2009)	1728	Batang Gadis NP	Pig-tailed macaque	97	5.61	Low	0.00	0.983333	99.383333
(Wibisono et al., 2009)	1728	Batang Gadis NP	Wild boar	10	0.58	Low	0.00	0.983333	99.383333
(Wibisono et al., 2009)	1728	Batang Gadis NP	Bearded pig	0	0.00	Low	0.00	0.983333	99.383333

(T. N. E. Gray, 2018)	8236	Southern Cardamom NP	Long-tailed macaque	0	0.00	Low	0.00	11.783333	103.33333
(T. N. E. Gray, 2018)	8236	Southern Cardamom NP	Wild boar	260	3.16	Low	0.00	11.783333	103.33333
HKK ForestGEO Project*	12807	Huai Kha Khaeng WS	Long-tailed macaque	0	0.00	Low	0.00	15.6324	99.217
HKK ForestGEO Project*	12807	Huai Kha Khaeng WS	Wild boar	807	6.30	Low	0.00	15.6324	99.217
(Luskin, Brashares, et al., 2017)	2533	Kerinci Seblat	Long-tailed macaque	56	2.21	High	39.69	–1.49227	101.54705
(Luskin, Brashares, et al., 2017)	2533	Kerinci Seblat	Pig-tailed macaque	1454	57.40	High	39.69	–1.49227	101.54705
(Luskin, Brashares, et al., 2017)	2533	Kerinci Seblat	Bearded pig	67	2.65	High	39.69	–1.49227	101.54705
(Luskin, Brashares, et al., 2017)	2533	Kerinci Seblat	Wild boar	820	32.37	High	39.69	–1.49227	101.54705
(Gibson et al., 2013)	10236	Khlong Saeng WS	Long-tailed macaque	28	0.27	Low	0.00	9.1946855	98.589278
(Gibson et al., 2013)	10236	Khlong Saeng WS	Pig-tailed macaque	35	0.34	Low	0.00	9.1946855	98.589278
(Gibson et al., 2013)	10236	Khlong Saeng WS	Wild boar	1478	14.44	Low	0.00	9.1946855	98.589278

Therese Lamperty*	4972	Singapore CCNR	Long-tailed macaque	284	5.71	Low	0.04	1.3548753	103.77899
Therese Lamperty*	4972	Singapore CCNR	Pig-tailed macaque	0	0.00	Low	0.04	1.3548753	103.77899
Therese Lamperty*	4972	Singapore CCNR	Bearded pig	0	0.00	Low	0.04	1.3548753	103.77899
Therese Lamperty*	4972	Singapore CCNR	Wild boar	217	4.36	Low	0.04	1.3548753	103.77899
Therese Lamperty*	14725	Singapore CCNR	Pig-tailed macaque	0	0.00	Low	0.10	1.3574095	103.78249
Therese Lamperty*	14725	Singapore CCNR	Bearded pig	0	0.00	Low	0.10	1.3574095	103.78249
Therese Lamperty*	14725	Singapore CCNR	Wild boar	69	0.47	Low	0.10	1.3574095	103.78249
Therese Lamperty*	14725	Singapore CCNR	Long-tailed macaque	327	2.22	Low	0.10	1.3574095	103.78249
Therese Lamperty*	6080	Singapore CCNR	Pig-tailed macaque	0	0.00	Low	0.08	1.356403	103.78162
Therese Lamperty*	6080	Singapore CCNR	Wild boar	278	4.57	Low	0.08	1.356403	103.78162
Therese Lamperty*	6080	Singapore CCNR	Long-tailed macaque	759	12.48	Low	0.08	1.356403	103.78162
Therese Lamperty*	6080	Singapore CCNR	Bearded pig	0	0.00	Low	0.08	1.356403	103.78162
Therese Lamperty*	32522	Singapore CCNR	Bearded pig	0	0.00	Low	0.10	1.356981	103.78353
Therese Lamperty*	32522	Singapore CCNR	Pig-tailed macaque	0	0.00	Low	0.10	1.356981	103.78353
Therese Lamperty*	32522	Singapore CCNR	Wild boar	107	0.33	Low	0.10	1.356981	103.78353

Therese Lamperty*	32522	Singapore CCNR	Long-tailed macaque	554	1.70	Low	0.10	1.356981	103.78353
Therese Lamperty*	2916	Singapore CCNR	Bearded pig	0	0.00	Low	0.10	1.3569344	103.78374
Therese Lamperty*	2916	Singapore CCNR	Pig-tailed macaque	0	0.00	Low	0.10	1.3569344	103.78374
Therese Lamperty*	2916	Singapore CCNR	Wild boar	219	7.51	Low	0.10	1.3569344	103.78374
Therese Lamperty*	2916	Singapore CCNR	Long-tailed macaque	389	13.34	Low	0.10	1.3569344	103.78374
Therese Lamperty*	208	Singapore CCNR	Pig-tailed macaque	0	0.00	Low	0.23	1.363678	103.78155
Therese Lamperty*	208	Singapore CCNR	Wild boar	44	21.15	Low	0.23	1.363678	103.78155
Therese Lamperty*	208	Singapore CCNR	Bearded pig	0	0.00	Low	0.23	1.363678	103.78155
Therese Lamperty*	208	Singapore CCNR	Long-tailed macaque	25	12.02	Low	0.23	1.363678	103.78155
Therese Lamperty*	5103	Singapore CCNR	Long-tailed macaque	1152	22.57	Low	0.55	1.3781586	103.80069
Therese Lamperty*	5103	Singapore CCNR	Pig-tailed macaque	0	0.00	Low	0.55	1.3781586	103.80069
Therese Lamperty*	5103	Singapore CCNR	Bearded pig	0	0.00	Low	0.55	1.3781586	103.80069
Therese Lamperty*	5103	Singapore CCNR	Wild boar	1199	23.50	Low	0.55	1.3781586	103.80069
Therese Lamperty*	4482	Singapore CCNR	Bearded pig	0	0.00	Low	0.39	1.366403	103.80259
Therese Lamperty*	4482	Singapore CCNR	Pig-tailed macaque	0	0.00	Low	0.39	1.366403	103.80259

Therese Lamperty*	4482	Singapore CCNR	Long-tailed macaque	283	6.31	Low	0.39	1.366403	103.80259
Therese Lamperty*	4482	Singapore CCNR	Wild boar	242	5.40	Low	0.39	1.366403	103.80259
Therese Lamperty*	3954	Singapore CCNR	Pig-tailed macaque	0	0.00	Low	0.62	1.380912	103.7973
Therese Lamperty*	3954	Singapore CCNR	Long-tailed macaque	311	7.87	Low	0.62	1.380912	103.7973
Therese Lamperty*	3954	Singapore CCNR	Bearded pig	0	0.00	Low	0.62	1.380912	103.7973
Therese Lamperty*	3954	Singapore CCNR	Wild boar	117	2.96	Low	0.62	1.380912	103.7973
Therese Lamperty*	18276	Singapore CCNR	Long-tailed macaque	321	1.76	Low	0.56	1.3774918	103.79633
Therese Lamperty*	18276	Singapore CCNR	Bearded pig	0	0.00	Low	0.56	1.3774918	103.79633
Therese Lamperty*	18276	Singapore CCNR	Wild boar	130	0.71	Low	0.56	1.3774918	103.79633
Therese Lamperty*	18276	Singapore CCNR	Pig-tailed macaque	0	0.00	Low	0.56	1.3774918	103.79633
Therese Lamperty*	28089	Singapore CCNR	Pig-tailed macaque	0	0.00	Low	0.43	1.3717492	103.80055
Therese Lamperty*	28089	Singapore CCNR	Long-tailed macaque	3067	10.92	Low	0.43	1.3717492	103.80055
Therese Lamperty*	28089	Singapore CCNR	Bearded pig	0	0.00	Low	0.43	1.3717492	103.80055
Therese Lamperty*	28089	Singapore CCNR	Wild boar	2124	7.56	Low	0.43	1.3717492	103.80055
Therese Lamperty*	3236	Singapore CCNR	Bearded pig	0	0.00	Low	0.57	1.3786058	103.79018

Therese Lamperty*	3236	Singapore CCNR	Pig-tailed macaque	0	0.00	Low	0.57	1.3786058	103.79018
Therese Lamperty*	3236	Singapore CCNR	Long-tailed macaque	512	15.82	Low	0.57	1.3786058	103.79018
Therese Lamperty*	3236	Singapore CCNR	Wild boar	87	2.69	Low	0.57	1.3786058	103.79018
Therese Lamperty*	994	Singapore CCNR	Bearded pig	0	0.00	Low	0.57	1.3785495	103.78994
Therese Lamperty*	994	Singapore CCNR	Wild boar	22	2.21	Low	0.57	1.3785495	103.78994
Therese Lamperty*	994	Singapore CCNR	Pig-tailed macaque	0	0.00	Low	0.57	1.3785495	103.78994
Therese Lamperty*	994	Singapore CCNR	Long-tailed macaque	104	10.46	Low	0.57	1.3785495	103.78994
Megan Baker*	563	Don Yai Wildlife Sanctuary	Long-tailed macaque	0	0.00	Low	0.00	14.078057	101.96441
Megan Baker*	563	Don Yai Wildlife Sanctuary	Wild boar	81	14.39	Low	0.00	14.078057	101.96441
Bill McShea*	2581	Huai Kha Khaeng Wildlife Sanctuary	Wild boar	1058	40.99	Low	0.00	15.631211	99.218792
Bill McShea*	2581	Huai Kha Khaeng Wildlife Sanctuary	Long-tailed macaque	1	0.04	Low	0.00	15.631211	99.218792
Jedediah Brodie*	1499	Hose mtns	Bearded pig	196	13.08	Low	0.00	2.2310389	113.68621

Jedediah Brodie*	1499	Hose mtns	Long-tailed macaque	26	1.73	Low	0.00	2.2310389	113.68621
Jedediah Brodie*	1499	Hose mtns	Pig-tailed macaque	286	19.08	Low	0.00	2.2310389	113.68621
Megan Baker*	3177	Huai Kha Khaeng Wildlife Sanctuary	Long-tailed macaque	17	0.54	Low	0.00	14.551925	100.02348
(Luskin, Albert, et al., 2017)	6425	Kerinci Seblat	Long-tailed macaque	286	4.45	High	31.03	–1.521746	101.49151
(Luskin, Albert, et al., 2017)	6425	Kerinci Seblat	Pig-tailed macaque	6889	107.22	High	31.03	–1.521746	101.49151
(Luskin, Albert, et al., 2017)	6425	Kerinci Seblat	Bearded pig	261	4.06	High	31.03	–1.521746	101.49151
(Luskin, Albert, et al., 2017)	6425	Kerinci Seblat	Wild boar	1368	21.29	High	31.03	–1.521746	101.49151
Luskin*	4823	KhaoChong	Wild boar	163	3.38	Low	0.00	7.5254368	99.804522
Luskin*	4823	KhaoChong	Long-tailed macaque	0	0.00	Low	0.00	7.5254368	99.804522
Luskin*	4823	KhaoChong	Pig-tailed macaque	562	11.65	Low	0.00	7.5254368	99.804522
Luskin*	4404	Khao Yai NP	Long-tailed macaque	0	0.00	Low	0.00	14.439673	101.36817
Luskin*	4404	Khao Yai NP	Wild boar	267	6.06	Low	0.00	14.439673	101.36817

(Luskin, Albert, et al., 2017)	414	Gunung Leuser	Long-tailed macaque	72	17.39	High	21.23	3.7659143	98.08757
(Luskin, Albert, et al., 2017)	414	Gunung Leuser	Pig-tailed macaque	178	43.00	High	21.23	3.7659143	98.08757
(Luskin, Albert, et al., 2017)	414	Gunung Leuser	Wild boar	352	85.02	High	21.23	3.7659143	98.08757
Jedediah Brodie*	8038	Maliau	Long-tailed macaque	6	0.07	Low	0.00	4.7259108	116.93412
Jedediah Brodie*	8038	Maliau	Bearded pig	2709	33.70	Low	0.00	4.7259108	116.93412
Jedediah Brodie*	8038	Maliau	Pig-tailed macaque	631	7.85	Low	0.00	4.7259108	116.93412
Jedediah Brodie*	2315	Mulu	Bearded pig	95	4.10	Low	0.00	4.0991694	114.88089
Jedediah Brodie*	2315	Mulu	Pig-tailed macaque	39	1.68	Low	0.00	4.0991694	114.88089
Jedediah Brodie*	2315	Mulu	Long-tailed macaque	3	0.13	Low	0.00	4.0991694	114.88089
(Takeuchi et al., 2021)	2794	Pasoh	Wild boar	669	23.94	High	34.86	3.0355647	102.32117
(Takeuchi et al., 2021)	2794	Pasoh	Bearded pig	0	0.00	High	34.86	3.0355647	102.32117
(Takeuchi et al., 2021)	2794	Pasoh	Pig-tailed macaque	847	30.31	High	34.86	3.0355647	102.32117
(Takeuchi et al., 2021)	2794	Pasoh	Long-tailed macaque	24	0.86	High	34.86	3.0355647	102.32117

(Takeuchi et al., 2021)	10534	Pasoh	Pig-tailed macaque	3018	28.65	High	34.60	3.0340595	102.32165
(Takeuchi et al., 2021)	10534	Pasoh	Bearded pig	0	0.00	High	34.60	3.0340595	102.32165
(Takeuchi et al., 2021)	10534	Pasoh	Wild boar	2039	19.36	High	34.60	3.0340595	102.32165
(Takeuchi et al., 2021)	10534	Pasoh	Long-tailed macaque	167	1.59	High	34.60	3.0340595	102.32165
(Takeuchi et al., 2021)	1661	Pasoh	Pig-tailed macaque	488	29.38	High	33.79	3.0311194	102.3195
(Takeuchi et al., 2021)	1661	Pasoh	Bearded pig	0	0.00	High	33.79	3.0311194	102.3195
(Takeuchi et al., 2021)	1661	Pasoh	Wild boar	244	14.69	High	33.79	3.0311194	102.3195
(Takeuchi et al., 2021)	1661	Pasoh	Long-tailed macaque	20	1.20	High	33.79	3.0311194	102.3195
TEAM*	1740	Pasoh	Pig-tailed macaque	1534	88.16	High	36.01	3.0442023	102.31948
TEAM*	1740	Pasoh	Long-tailed macaque	31	1.78	High	36.01	3.0442023	102.31948
TEAM*	1740	Pasoh	Wild boar	533	30.63	High	36.01	3.0442023	102.31948
TEAM*	1740	Pasoh	Bearded pig	0	0.00	High	36.01	3.0442023	102.31948
TEAM*	1710	Pasoh	Wild boar	456	26.67	High	35.73	3.0417915	102.32002
TEAM*	1710	Pasoh	Pig-tailed macaque	854	49.94	High	35.73	3.0417915	102.32002
TEAM*	1710	Pasoh	Bearded pig	0	0.00	High	35.73	3.0417915	102.32002

TEAM*	1710	Pasoh	Long-tailed macaque	10	0.58	High	35.73	3.0417915	102.32002
TEAM*	1770	Pasoh	Long-tailed macaque	24	1.36	High	35.96	3.0424549	102.32068
TEAM*	1770	Pasoh	Pig-tailed macaque	836	47.23	High	35.96	3.0424549	102.32068
TEAM*	1770	Pasoh	Wild boar	674	38.08	High	35.96	3.0424549	102.32068
TEAM*	1770	Pasoh	Bearded pig	0	0.00	High	35.96	3.0424549	102.32068
Jedediah Brodie*	3217	Pulong Tau	Pig-tailed macaque	131	4.07	Low	0.00	3.8277281	115.49439
Jedediah Brodie*	3217	Pulong Tau	Bearded pig	254	7.90	Low	0.00	3.8277281	115.49439
Jedediah Brodie*	3217	Pulong Tau	Long-tailed macaque	0	0.00	Low	0.00	3.8277281	115.49439
Therese Lamperty*	1401	Singapore Sentosa S Ridges	Long-tailed macaque	0	0.00	Low	0.00	1.2657539	103.81049
Therese Lamperty*	1401	Singapore Sentosa S Ridges	Bearded pig	0	0.00	Low	0.00	1.2657539	103.81049
Therese Lamperty*	1401	Singapore Sentosa S Ridges	Pig-tailed macaque	0	0.00	Low	0.00	1.2657539	103.81049
Therese Lamperty*	1401	Singapore Sentosa S Ridges	Wild boar	0	0.00	Low	0.00	1.2657539	103.81049
Megan Baker*	1193	Ta Phraya National Park	Wild boar	51	4.27	Low	0.00	14.136116	102.64964

Megan Baker*	1193	Ta Phraya National Park	Long-tailed macaque	0	0.00	Low	0.00	14.136116	102.64964
Jedediah Brodie*	1410	Ulu Baram	Bearded pig	38	2.70	Low	0.00	3.2992088	115.22276
Jedediah Brodie*	1410	Ulu Baram	Long-tailed macaque	2	0.14	Low	0.00	3.2992088	115.22276
Jedediah Brodie*	1410	Ulu Baram	Pig-tailed macaque	302	21.42	Low	0.00	3.2992088	115.22276
(Tan et al., 2017)	4242	Ulu Muda	Long-tailed macaque	0	0.00	Low	0.00	6.0962252	101.00221
(Tan et al., 2017)	4242	Ulu Muda	Pig-tailed macaque	603	14.21	Low	0.00	6.0962252	101.00221
(Tan et al., 2017)	4242	Ulu Muda	Bearded pig	0	0.00	Low	0.00	6.0962252	101.00221
(Tan et al., 2017)	4242	Ulu Muda	Wild boar	926	21.83	Low	0.00	6.0962252	101.00221
(Tan et al., 2017)	13110	Ulu Muda	Wild boar	4264	32.52	Low	0.00	6.1012236	101.00332
(Tan et al., 2017)	13110	Ulu Muda	Bearded pig	0	0.00	Low	0.00	6.1012236	101.00332
(Tan et al., 2017)	13110	Ulu Muda	Pig-tailed macaque	2179	16.62	Low	0.00	6.1012236	101.00332
(Tan et al., 2017)	13110	Ulu Muda	Long-tailed macaque	0	0.00	Low	0.00	6.1012236	101.00332
(Tan et al., 2017)	5645	Ulu Muda	Long-tailed macaque	0	0.00	Low	0.00	6.0994284	100.99997
(Tan et al., 2017)	5645	Ulu Muda	Wild boar	850	15.06	Low	0.00	6.0994284	100.99997

(Tan et al., 2017)	5645	Ulu Muda	Pig-tailed macaque	1251	22.16	Low	0.00	6.0994284	100.99997
(Tan et al., 2017)	5645	Ulu Muda	Bearded pig	0	0.00	Low	0.00	6.0994284	100.99997
Jedediah Brodie*	1717	Ulu Padas	Long-tailed macaque	6	0.35	Low	0.00	4.3569756	115.7126
Jedediah Brodie*	1717	Ulu Padas	Pig-tailed macaque	294	17.12	Low	0.00	4.3569756	115.7126
Jedediah Brodie*	1717	Ulu Padas	Bearded pig	94	5.47	Low	0.00	4.3569756	115.7126
Jedediah Brodie*	1132	Ulu Trusan	Long-tailed macaque	11	0.97	Low	0.00	4.3869161	115.47177
Jedediah Brodie*	1132	Ulu Trusan	Pig-tailed macaque	160	14.13	Low	0.00	4.3869161	115.47177
Jedediah Brodie*	1132	Ulu Trusan	Bearded pig	83	7.33	Low	0.00	4.3869161	115.47177

***** Unpublished data sets.

Table S5.3. Capture rates of long-tailed macaque, pig-tailed macaque, wild boar and bearded pig with corresponding data sources and Forest Landscape Integrity Index (FLII) values. RAI, relative abundance index. FLII group was classified as high (FLII values 7–10) or low (FLII 0 to <7).

Source	**Trapping effort (camera nights)**	**Landscape**	**Species**	**Records**	**RAI**	**FLII group**	**Average FLII value 20 km**	**Latitude**	**Longitude**
(T. N. E. Gray & Channa, 2011)	2717	Phnom Prich WS	Wild boar	155	5.70	Intact	8.89	12.801	106.501
(T. N. E. Gray & Channa, 2011)	2717	Phnom Prich WS	Long-tailed macaque	2	0.07	Intact	8.89	12.801	106.501
(Clements, 2013)	21780	Terengganu	Wild boar	663	3.04	Degraded	6.46	5.014865	102.551272
(Clements, 2013)	21780	Terengganu	Bearded pig	0	0.00	Degraded	6.46	5.014865	102.551272
(Clements, 2013)	21780	Terengganu	Pig-tailed macaque	123	0.56	Degraded	6.46	5.014865	102.551272
(Clements, 2013)	21780	Terengganu	Long-tailed macaque	546	2.51	Degraded	6.46	5.014865	102.551272
(Clements, 2013)	25904	Perak	Wild boar	4168	16.09	Degraded	5.48	5.5	101
(Clements, 2013)	25904	Perak	Bearded pig	0	0.00	Degraded	5.48	5.5	101
(Clements, 2013)	25904	Perak	Pig-tailed macaque	402	1.55	Degraded	5.48	5.5	101
(Clements, 2013)	25904	Perak	Long-tailed macaque	169	0.65	Degraded	5.48	5.5	101
(Clements, 2013)	16066	Terengganu	Wild boar	510	3.17	Degraded	6.46	5.014865	102.551272
(Clements, 2013)	16066	Terengganu	Long-tailed macaque	75	0.47	Degraded	6.46	5.014865	102.551272

(Clements, 2013)	16066	Terengganu	Pig-tailed macaque	30	0.19	Degraded	6.46	5.014865	102.551272
(Clements, 2013)	16066	Terengganu	Bearded pig	0	0.00	Degraded	6.46	5.014865	102.551272
(Luskin, Brashares, et al., 2017)	590	Kerinci Seblat	Bearded pig	1	0.17	Degraded	5.75	–1.38184	101.30522
(Luskin, Brashares, et al., 2017)	590	Kerinci Seblat	Pig-tailed macaque	51	8.64	Degraded	5.75	–1.38184	101.30522
(Luskin, Brashares, et al., 2017)	590	Kerinci Seblat	Long-tailed macaque	0	0.00	Degraded	5.75	–1.38184	101.30522
(Luskin, Brashares, et al., 2017)	590	Kerinci Seblat	Wild boar	16	2.71	Degraded	5.75	–1.38184	101.30522
(Linkie, 2006)	1849	Kerinci Seblat	Bearded pig	5	0.27	Degraded	5.75	–1.38184	101.30522
(Linkie, 2006)	1849	Kerinci Seblat	Pig-tailed macaque	43	2.33	Degraded	5.75	–1.38184	101.30522
(Linkie, 2006)	1849	Kerinci Seblat	Wild boar	11	0.59	Degraded	5.75	–1.38184	101.30522
(Linkie, 2006)	1849	Kerinci Seblat	Long-tailed macaque	0	0.00	Degraded	5.75	–1.38184	101.30522
(Cheyne & Macdonald, 2011)	22588	Sabangau	Bearded pig	147	0.65	Degraded	5.79	–2.333161765	113.8917188
(Cheyne & Macdonald, 2011)	22588	Sabangau	Long-tailed macaque	4	0.02	Degraded	5.79	–2.333161765	113.8917188
(Cheyne & Macdonald, 2011)	22588	Sabangau	Pig-tailed macaque	512	2.27	Degraded	5.79	–2.333161765	113.8917188
(Yue et al., 2015)	854	Ulu Segama	Long-tailed macaque	12	1.41	Intact	9.25	5.006915	117.731993
(Yue et al., 2015)	854	Ulu Segama	Pig-tailed macaque	60	7.03	Intact	9.25	5.006915	117.731993
(Yue et al., 2015)	854	Ulu Segama	Bearded pig	240	28.10	Intact	9.25	5.006915	117.731993

(Yue et al., 2015)	1299	Ulu Segama	Long-tailed macaque	1	0.08	Degraded	6.81	4.768259	117.865257
(Yue et al., 2015)	1299	Ulu Segama	Pig-tailed macaque	47	3.62	Degraded	6.81	4.768259	117.865257
(Yue et al., 2015)	1299	Ulu Segama	Bearded pig	132	10.16	Degraded	6.81	4.768259	117.865257
(Sunarto, 2011)	7513	Riau Province	Wild boar	112	1.49	Degraded	6.96	–0.921494	102.385766
(Sunarto, 2011)	7513	Riau Province	Bearded pig	27	0.36	Degraded	6.96	–0.921494	102.385766
(Sunarto, 2011)	7513	Riau Province	Pig-tailed macaque	607	8.08	Degraded	6.96	–0.921494	102.385766
(Sunarto, 2011)	7513	Riau Province	Long-tailed macaque	10	0.13	Degraded	6.96	–0.921494	102.385766
(Bernard et al., 2013)	1436	Imbak Canyon Conservation Area	Bearded pig	92	6.41	Degraded	4.60	5.157041	116.929858
(Bernard et al., 2013)	1436	Imbak Canyon Conservation Area	Pig-tailed macaque	76	5.29	Degraded	4.60	5.157041	116.929858
(Bernard et al., 2013)	1436	Imbak Canyon Conservation Area	Long-tailed macaque	8	0.56	Degraded	4.60	5.157041	116.929858
(O’Brien et al., 2003)	9095	Bukit Barisan Selatan	Long-tailed macaque	2	0.02	Intact	7.55	–5.769091596	104.5371698
(O’Brien et al., 2003)	9095	Bukit Barisan Selatan	Pig-tailed macaque	169	1.86	Intact	7.55	–5.769091596	104.5371698
(O’Brien et al., 2003)	9095	Bukit Barisan Selatan	Wild boar	162	1.78	Intact	7.55	–5.769091596	104.5371698
(O’Brien et al., 2003)	3030	Bukit Barisan Selatan	Long-tailed macaque	0	0.00	Degraded	6.57	–4.89291945	103.8093489
(O’Brien et al., 2003)	3030	Bukit Barisan Selatan	Pig-tailed macaque	102	3.37	Degraded	6.57	–4.89291945	103.8093489

(O’Brien et al., 2003)	3030	Bukit Barisan Selatan	Wild boar	96	3.17	Degraded	6.57	–4.89291945	103.8093489
(O’Brien et al., 2003)	8409	Bukit Barisan Selatan	Long-tailed macaque	1	0.01	Degraded	6.62	–5.32691251	104.1986596
(O’Brien et al., 2003)	8409	Bukit Barisan Selatan	Pig-tailed macaque	171	2.03	Degraded	6.62	–5.32691251	104.1986596
(O’Brien et al., 2003)	8409	Bukit Barisan Selatan	Wild boar	119	1.42	Degraded	6.62	–5.32691251	104.1986596
(J. H. Moore et al., 2016)	512	Krau	Wild boar	7	1.37	Degraded	6.26	3.67332	102.08188
(J. H. Moore et al., 2016)	512	Krau	Bearded pig	0	0.00	Degraded	6.26	3.67332	102.08188
(J. H. Moore et al., 2016)	512	Krau	Long-tailed macaque	0	0.00	Degraded	6.26	3.67332	102.08188
(J. H. Moore et al., 2016)	512	Krau	Pig-tailed macaque	40	7.81	Degraded	6.26	3.67332	102.08188
(J. H. Moore et al., 2016)	512	Krau	Bearded pig	0	0.00	Degraded	6.96	3.71777	102.1288
(J. H. Moore et al., 2016)	512	Krau	Long-tailed macaque	1	0.20	Degraded	6.96	3.71777	102.1288
(J. H. Moore et al., 2016)	512	Krau	Pig-tailed macaque	111	21.68	Degraded	6.96	3.71777	102.1288
(J. H. Moore et al., 2016)	512	Krau	Wild boar	16	3.13	Degraded	6.96	3.71777	102.1288

(Haidir et al., 2018)	8399	Kerinci Seblat	Long-tailed macaque	0	0.00	Degraded	6.70	–1.870837	101.887209
(Haidir et al., 2018)	8399	Kerinci Seblat	Wild boar	39	0.46	Degraded	6.70	–1.870837	101.887209
(Haidir et al., 2018)	8399	Kerinci Seblat	Pig-tailed macaque	413	4.92	Degraded	6.70	–1.870837	101.887209
(Haidir et al., 2018)	8399	Kerinci Seblat	Bearded pig	0	0.00	Degraded	6.70	–1.870837	101.887209
(Haidir et al., 2018)	7053	Kerinci Seblat	Wild boar	32	0.45	Degraded	6.33	–2.264451	101.794251
(Haidir et al., 2018)	7053	Kerinci Seblat	Bearded pig	1	0.01	Degraded	6.33	–2.264451	101.794251
(Haidir et al., 2018)	7053	Kerinci Seblat	Pig-tailed macaque	606	8.59	Degraded	6.33	–2.264451	101.794251
(Haidir et al., 2018)	7053	Kerinci Seblat	Long-tailed macaque	0	0.00	Degraded	6.33	–2.264451	101.794251
(Haidir et al., 2018)	6674	Kerinci Seblat	Wild boar	43	0.64	Degraded	6.12	–2.031408	101.126884
(Haidir et al., 2018)	6674	Kerinci Seblat	Bearded pig	100	1.50	Degraded	6.12	–2.031408	101.126884
(Haidir et al., 2018)	6674	Kerinci Seblat	Long-tailed macaque	0	0.00	Degraded	6.12	–2.031408	101.126884
(Haidir et al., 2018)	6674	Kerinci Seblat	Pig-tailed macaque	54	0.81	Degraded	6.12	–2.031408	101.126884
(Haidir et al., 2018)	6278	Kerinci Seblat	Pig-tailed macaque	373	5.94	Intact	7.40	–3.024615	101.950937
(Haidir et al., 2018)	6278	Kerinci Seblat	Long-tailed macaque	0	0.00	Intact	7.40	–3.024615	101.950937

(Haidir et al., 2018)	6278	Kerinci Seblat	Bearded pig	294	4.68	Intact	7.40	–3.024615	101.950937
(Haidir et al., 2018)	6278	Kerinci Seblat	Wild boar	73	1.16	Intact	7.40	–3.024615	101.950937
(Beaudrot et al., 2019)	522	Nam Kading	Wild boar	13	2.49	Degraded	5.13	18.316667	104.01
(Beaudrot et al., 2019)	817	Nam Kading	Wild boar	34	4.16	Degraded	5.13	18.316667	104.01
(Beaudrot et al., 2019)	679	Nam Kading	Wild boar	25	3.68	Degraded	5.13	18.316667	104.01
(Beaudrot et al., 2019)	792	Nam Kading	Wild boar	50	6.31	Degraded	5.13	18.316667	104.01
(Beaudrot et al., 2019)	768	Nam Kading	Wild boar	27	3.52	Degraded	5.13	18.316667	104.01
(Beaudrot et al., 2019)	766	Nam Kading	Wild boar	38	4.96	Degraded	5.13	18.316667	104.01
(Onoguchi & Matsubayashi, 2008)	551	Deramakot FR	Long-tailed macaque	1	0.18	Intact	7.97	5.3501	117.401
(Onoguchi & Matsubayashi, 2008)	551	Deramakot FR	Pig-tailed macaque	17	3.09	Intact	7.97	5.3501	117.401
(Onoguchi & Matsubayashi, 2008)	551	Deramakot FR	Bearded pig	16	2.90	Intact	7.97	5.3501	117.401
(Onoguchi & Matsubayashi, 2008)	272	Tangkulap FR	Pig-tailed macaque	4	1.47	Degraded	6.94	5.4401	117.201
(Onoguchi & Matsubayashi, 2008)	272	Tangkulap FR	Long-tailed macaque	1	0.37	Degraded	6.94	5.4401	117.201

(Onoguchi & Matsubayashi, 2008)	272	Tangkulap FR	Bearded pig	8	2.94	Degraded	6.94	5.4401	117.201
(Mohd-Azlan & Engkamat, 2006)	1127	Lambir Hills NP	Pig-tailed macaque	63	5.59	Degraded	1.58	4.189875	114.018566
(Mohd-Azlan & Engkamat, 2006)	1127	Lambir Hills NP	Bearded pig	1	0.09	Degraded	1.58	4.189875	114.018566
(Mohd-Azlan & Engkamat, 2006)	1127	Lambir Hills NP	Long-tailed macaque	1	0.09	Degraded	1.58	4.189875	114.018566
(Grassman et al., 2006)	1224	Phu Khieo WS	Long-tailed macaque	0	0.00	Intact	9.65	16.401	101.401
(Grassman et al., 2006)	1224	Phu Khieo WS	Wild boar	40	3.27	Intact	9.65	16.401	101.401
(Srikosamatara, 1993)	1000	Huai Kha Khaeng WS	Wild boar	2	0.20	Intact	8.11	15.708765	99.420847
(Srikosamatara, 1993)	1000	Huai Kha Khaeng WS	Long-tailed macaque	0	0.00	Intact	8.11	15.708765	99.420847
(Van Schaik & Griffiths, 1996)	2000	Gunung Leuser	Long-tailed macaque	0	0.00	Intact	8.26	3.201005556	97.40342778
(Van Schaik & Griffiths, 1996)	2000	Gunung Leuser	Pig-tailed macaque	7	0.35	Intact	8.26	3.201005556	97.40342778
(Van Schaik & Griffiths, 1996)	2000	Gunung Leuser	Wild boar	24	1.20	Intact	8.26	3.201005556	97.40342778

(Van Schaik & Griffiths, 1996)	1000	Ujung Kulon NP	Long-tailed macaque	0	0.00	Intact	8.70	–6.666667	105.333333
(Van Schaik & Griffiths, 1996)	1000	Ujung Kulon NP	Wild boar	302	30.20	Intact	8.70	–6.666667	105.333333
(Kawanishi & Sunquist, 2004)	4336	Merapoh	Wild boar	132	3.04	Intact	7.01	4.703779	102.039437
(Kawanishi & Sunquist, 2004)	4336	Merapoh	Long-tailed macaque	1	0.02	Intact	7.01	4.703779	102.039437
(Kawanishi & Sunquist, 2004)	4336	Merapoh	Bearded pig	0	0.00	Intact	7.01	4.703779	102.039437
(Kawanishi & Sunquist, 2004)	4336	Merapoh	Pig-tailed macaque	11	0.25	Intact	7.01	4.703779	102.039437
Kawanishi & Sunquist (2004)	4847	Taman Negara	Long-tailed macaque	0	0.00	Intact	7.71	4.388255	102.397294
(Kawanishi & Sunquist, 2004)	4847	Taman Negara	Bearded pig	0	0.00	Intact	7.71	4.388255	102.397294
(Kawanishi & Sunquist, 2004)	4847	Taman Negara	Wild boar	117	2.41	Intact	7.71	4.388255	102.397294
(Kawanishi & Sunquist, 2004)	4847	Taman Negara	Pig-tailed macaque	3	0.06	Intact	7.71	4.388255	102.397294

(Kawanishi & Sunquist, 2004)	4871	Taman Negara	Wild boar	256	5.26	Degraded	5.98	4.927198	102.424521
(Kawanishi & Sunquist, 2004)	4871	Taman Negara	Long-tailed macaque	0	0.00	Degraded	5.98	4.927198	102.424521
(Kawanishi & Sunquist, 2004)	4871	Taman Negara	Pig-tailed macaque	26	0.53	Degraded	5.98	4.927198	102.424521
(Kawanishi & Sunquist, 2004)	4871	Taman Negara	Bearded pig	0	0.00	Degraded	5.98	4.927198	102.424521
(Novarino, 2005)	2720	Taratak Sungai Lundang	Bearded pig	0	0.00	Intact	7.45	–1.043164	100.5400619
(Novarino, 2005)	2720	Taratak Sungai Lundang	Long-tailed macaque	22	0.81	Intact	7.45	–1.043164	100.5400619
(Novarino, 2005)	2720	Taratak Sungai Lundang	Pig-tailed macaque	119	4.38	Intact	7.45	–1.043164	100.5400619
(Novarino, 2005)	2720	Taratak Sungai Lundang	Wild boar	29	1.07	Intact	7.45	–1.043164	100.5400619
(Azlan J, 2006)	5972	Jerangau FR	Bearded pig	0	0.00	Degraded	3.29	4.861019	103.163741
(Azlan J, 2006)	5972	Jerangau FR	Long-tailed macaque	21	0.35	Degraded	3.29	4.861019	103.163741
(Azlan J, 2006)	5972	Jerangau FR	Wild boar	774	12.96	Degraded	3.29	4.861019	103.163741

(Azlan J, 2006)	5972	Jerangau FR	Pig-tailed macaque	91	1.52	Degraded	3.29	4.861019	103.163741
(Maddox et al., 2007)	7102	PT Asiatic Persada	Long-tailed macaque	67	0.94	Degraded	2.35	–1.91525	103.346343
(Maddox et al., 2007)	7102	PT Asiatic Persada	Wild boar	1861	26.20	Degraded	2.35	–1.91525	103.346343
(Maddox et al., 2007)	7102	PT Asiatic Persada	Pig-tailed macaque	855	12.04	Degraded	2.35	–1.91525	103.346343
(Maddox et al., 2007)	7102	PT Asiatic Persada	Bearded pig	442	6.22	Degraded	2.35	–1.91525	103.346343
(D. M. Rayan, 2007)	2664	Gunung Basor FR	Pig-tailed macaque	45	1.69	Intact	7.12	5.470098	101.824206
(D. M. Rayan, 2007)	2664	Gunung Basor FR	Long-tailed macaque	0	0.00	Intact	7.12	5.470098	101.824206
(D. M. Rayan, 2007)	2664	Gunung Basor FR	Wild boar	311	11.67	Intact	7.12	5.470098	101.824206
(D. M. Rayan, 2007)	2664	Gunung Basor FR	Bearded pig	0	0.00	Intact	7.12	5.470098	101.824206
(Lynam et al., 2007)	785	Temenggor	Wild boar	16	2.04	Intact	8.28	5.491777	101.583953
(Lynam et al., 2007)	785	Temenggor	Long-tailed macaque	0	0.00	Intact	8.28	5.491777	101.583953
(Lynam et al., 2007)	785	Temenggor	Pig-tailed macaque	13	1.66	Intact	8.28	5.491777	101.583953
(Lynam et al., 2007)	785	Temenggor	Bearded pig	0	0.00	Intact	8.28	5.491777	101.583953
(Lynam et al., 2007)	646	Bintang Hijau	Bearded pig	0	0.00	Degraded	6.46	5.459951	100.906538

(Lynam et al., 2007)	646	Bintang Hijau	Long-tailed macaque	0	0.00	Degraded	6.46	5.459951	100.906538
(Lynam et al., 2007)	646	Bintang Hijau	Wild boar	34	5.26	Degraded	6.46	5.459951	100.906538
(Lynam et al., 2007)	646	Bintang Hijau	Pig-tailed macaque	2	0.31	Degraded	6.46	5.459951	100.906538
(Lynam et al., 2007)	467	Jengai	Pig-tailed macaque	2	0.43	Intact	7.97	4.487744	103.06265
(Lynam et al., 2007)	467	Jengai	Wild boar	64	13.70	Intact	7.97	4.487744	103.06265
(Lynam et al., 2007)	467	Jengai	Long-tailed macaque	0	0.00	Intact	7.97	4.487744	103.06265
(Lynam et al., 2007)	467	Jengai	Bearded pig	0	0.00	Intact	7.97	4.487744	103.06265
(Lynam et al., 2007)	807	Jerteh	Long-tailed macaque	4	0.50	Degraded	3.73	5.591784	102.6123
(Lynam et al., 2007)	807	Jerteh	Bearded pig	0	0.00	Degraded	3.73	5.591784	102.6123
(Lynam et al., 2007)	807	Jerteh	Wild boar	131	16.23	Degraded	3.73	5.591784	102.6123
(Lynam et al., 2007)	807	Jerteh	Pig-tailed macaque	9	1.12	Degraded	3.73	5.591784	102.6123
(Lynam et al., 2007)	557	Taman Negara	Wild boar	59	10.59	Degraded	1.48	5.381286	102.176737
(Lynam et al., 2007)	557	Taman Negara	Bearded pig	0	0.00	Degraded	1.48	5.381286	102.176737
(Lynam et al., 2007)	557	Taman Negara	Long-tailed macaque	0	0.00	Degraded	1.48	5.381286	102.176737

(Lynam et al., 2007)	557	Taman Negara	Pig-tailed macaque	4	0.72	Degraded	1.48	5.381286	102.176737
(Lynam et al., 2007)	562	Ayer Ngah	Bearded pig	0	0.00	Degraded	1.26	5.76682	101.995568
(Lynam et al., 2007)	562	Ayer Ngah	Pig-tailed macaque	1	0.18	Degraded	1.26	5.76682	101.995568
(Lynam et al., 2007)	562	Ayer Ngah	Wild boar	129	22.95	Degraded	1.26	5.76682	101.995568
(Lynam et al., 2007)	562	Ayer Ngah	Long-tailed macaque	0	0.00	Degraded	1.26	5.76682	101.995568
(Lynam et al., 2007)	495	Cameron Highlands	Wild boar	6	1.21	Intact	7.73	4.571533	101.404658
(Lynam et al., 2007)	495	Cameron Highlands	Pig-tailed macaque	2	0.40	Intact	7.73	4.571533	101.404658
(Lynam et al., 2007)	495	Cameron Highlands	Bearded pig	0	0.00	Intact	7.73	4.571533	101.404658
(Lynam et al., 2007)	768	Taman Negara	Bearded pig	0	0.00	Intact	9.46	4.67491	102.567659
(Lynam et al., 2007)	768	Taman Negara	Pig-tailed macaque	1	0.13	Intact	9.46	4.67491	102.567659
(Lynam et al., 2007)	768	Taman Negara	Wild boar	10	1.30	Intact	9.46	4.67491	102.567659
(Lynam et al., 2007)	768	Taman Negara	Long-tailed macaque	0	0.00	Intact	9.46	4.67491	102.567659
(Lynam et al., 2007)	1172	Pekan	Pig-tailed macaque	11	0.94	Degraded	0.83	3.596469	103.095326
(Lynam et al., 2007)	1172	Pekan	Wild boar	11	0.94	Degraded	0.83	3.596469	103.095326
(Lynam et al., 2007)	1172	Pekan	Bearded pig	0	0.00	Degraded	0.83	3.596469	103.095326

(Lynam et al., 2007)	1172	Pekan	Long-tailed macaque	1	0.09	Degraded	0.83	3.596469	103.095326
(McShea et al., 2009)	5679	Bintulu acacia	Long-tailed macaque	2	0.04	Degraded	1.26	3.325328723	113.2678564
(McShea et al., 2009)	5679	Bintulu acacia	Pig-tailed macaque	105	1.85	Degraded	1.26	3.325328723	113.2678564
(McShea et al., 2009)	5679	Bintulu acacia	Bearded pig	68	1.20	Degraded	1.26	3.325328723	113.2678564
(Kitamura et al., 2010)	11106	Hala-bala WS	Pig-tailed macaque	237	2.13	Degraded	4.14	5.796887	101.812418
(Kitamura et al., 2010)	11106	Hala-bala WS	Wild boar	426	3.84	Degraded	4.14	5.796887	101.812418
(Kitamura et al., 2010)	11106	Hala-bala WS	Bearded pig	0	0.00	Degraded	4.14	5.796887	101.812418
(Kitamura et al., 2010)	11106	Hala-bala WS	Long-tailed macaque	0	0.00	Degraded	4.14	5.796887	101.812418
(Channa et al., 2010)	7295	Phnom Prich WS	Long-tailed macaque	0	0.00	Intact	9.69	12.936181	107.305066
(Channa et al., 2010)	7295	Phnom Prich WS	Wild boar	330	4.52	Intact	9.69	12.936181	107.305066
(Jenks et al., 2011)	6260	Khao Yai NP	Long-tailed macaque	0	0.00	Intact	8.38	14.441389	101.369722
(Jenks et al., 2011)	6260	Khao Yai NP	Wild boar	60	0.96	Intact	8.38	14.441389	101.369722

(Linkie, 2006)	2000	Kerinci Seblat	Wild boar	6	0.30	Intact	8.08	–2.416667	101.483333
(Linkie, 2006)	2000	Kerinci Seblat	Pig-tailed macaque	134	6.70	Intact	8.08	–2.416667	101.483333
(Linkie, 2006)	2000	Kerinci Seblat	Bearded pig	22	1.10	Intact	8.08	–2.416667	101.483333
(Linkie, 2006)	2000	Kerinci Seblat	Long-tailed macaque	0	0.00	Intact	8.08	–2.416667	101.483333
(Wibisono et al., 2009)	1728	Batang Gadis NP	Bearded pig	0	0.00	Intact	7.25	0.983333	99.383333
(Wibisono et al., 2009)	1728	Batang Gadis NP	Long-tailed macaque	5	0.29	Intact	7.25	0.983333	99.383333
(Wibisono et al., 2009)	1728	Batang Gadis NP	Wild boar	10	0.58	Intact	7.25	0.983333	99.383333
(Wibisono et al., 2009)	1728	Batang Gadis NP	Pig-tailed macaque	97	5.61	Intact	7.25	0.983333	99.383333
Kevin McLean CTFS*	877	Danum Valley	Bearded pig	12	1.37	Intact	9.25	4.95144	117.792
Kevin McLean CTFS*	877	Danum Valley	Pig-tailed macaque	45	5.13	Intact	9.25	4.95144	117.792
Kevin McLean CTFS*	877	Danum Valley	Long-tailed macaque	2	0.23	Intact	9.25	4.95144	117.792
(T. N. E. Gray, 2018)	8236	Southern Cardamom NP	Wild boar	260	3.16	Intact	8.98	11.783333	103.333333
(T. N. E. Gray, 2018)	8236	Southern Cardamom NP	Long-tailed macaque	0	0.00	Intact	8.98	11.783333	103.333333

HKK ForestGEO Project*	12807	Huai Kha Khaeng WS	Long-tailed macaque	0	0.00	Intact	9.75	15.6324	99.217
HKK ForestGEO Project*	12807	Huai Kha Khaeng WS	Wild boar	807	6.30	Intact	9.75	15.6324	99.217
(Luskin, Brashares, et al., 2017)	5759	Bukit Barisan Selatan	Long-tailed macaque	4	0.07	Intact	7.21	–5.29823	104.072475
(Luskin, Brashares, et al., 2017)	5759	Bukit Barisan Selatan	Pig-tailed macaque	541	9.39	Intact	7.21	–5.29823	104.072475
(Luskin, Brashares, et al., 2017)	5759	Bukit Barisan Selatan	Wild boar	450	7.81	Intact	7.21	–5.29823	104.072475
(Luskin, Brashares, et al., 2017)	2027	Kerinci Seblat	Long-tailed macaque	9	0.44	Degraded	5.82	–1.631883684	101.4381295
(Luskin, Brashares, et al., 2017)	2027	Kerinci Seblat	Pig-tailed macaque	250	12.33	Degraded	5.82	–1.631883684	101.4381295
(Luskin, Brashares, et al., 2017)	2027	Kerinci Seblat	Bearded pig	765	37.74	Degraded	5.82	–1.631883684	101.4381295
(Luskin, Brashares, et al., 2017)	2027	Kerinci Seblat	Wild boar	140	6.91	Degraded	5.82	–1.631883684	101.4381295
(Luskin, Brashares, et al., 2017)	2533	Kerinci Seblat	Long-tailed macaque	56	2.21	Degraded	3.77	–1.49227	101.54705

(Luskin, Brashares, et al., 2017)	2533	Kerinci Seblat	Pig-tailed macaque	1454	57.40	Degraded	3.77	–1.49227	101.54705
(Luskin, Brashares, et al., 2017)	2533	Kerinci Seblat	Bearded pig	67	2.65	Degraded	3.77	–1.49227	101.54705
(Luskin, Brashares, et al., 2017)	2533	Kerinci Seblat	Wild boar	820	32.37	Degraded	3.77	–1.49227	101.54705
(Gibson et al., 2013)	10236	Khlong Saeng WS	Long-tailed macaque	28	0.27	Intact	8.89	9.194685537	98.58927839
(Gibson et al., 2013)	10236	Khlong Saeng WS	Pig-tailed macaque	35	0.34	Intact	8.89	9.194685537	98.58927839
(Gibson et al., 2013)	10236	Khlong Saeng WS	Wild boar	1478	14.44	Intact	8.89	9.194685537	98.58927839
(Luskin, Albert, et al., 2017)	808	Bukit Barisan Selatan	Long-tailed macaque	3	0.37	Degraded	6.54	–5.358168041	104.1536392
(Luskin, Albert, et al., 2017)	808	Bukit Barisan Selatan	Pig-tailed macaque	270	33.42	Degraded	6.54	–5.358168041	104.1536392
(Luskin, Albert, et al., 2017)	808	Bukit Barisan Selatan	Wild boar	416	51.49	Degraded	6.54	–5.358168041	104.1536392
(Luskin, Albert, et al., 2017)	4875	Bukit Barisan Selatan	Wild boar	332	6.81	Intact	7.39	–5.256314328	104.1149463

(Luskin, Albert, et al., 2017)	4875	Bukit Barisan Selatan	Long-tailed macaque	1	0.02	Intact	7.39	–5.256314328	104.1149463
(Luskin, Albert, et al., 2017)	4875	Bukit Barisan Selatan	Pig-tailed macaque	1164	23.88	Intact	7.39	–5.256314328	104.1149463
Therese Lamperty*	4972	Singapore CCNR	Long-tailed macaque	284	5.71	Degraded	0.58	1.354875265	103.7789948
Therese Lamperty*	4972	Singapore CCNR	Pig-tailed macaque	0	0.00	Degraded	0.58	1.354875265	103.7789948
Therese Lamperty*	4972	Singapore CCNR	Bearded pig	0	0.00	Degraded	0.58	1.354875265	103.7789948
Therese Lamperty*	4972	Singapore CCNR	Wild boar	217	4.36	Degraded	0.58	1.354875265	103.7789948
Therese Lamperty*	14725	Singapore CCNR	Long-tailed macaque	327	2.22	Degraded	0.59	1.357409465	103.782489
Therese Lamperty*	14725	Singapore CCNR	Pig-tailed macaque	0	0.00	Degraded	0.59	1.357409465	103.782489
Therese Lamperty*	14725	Singapore CCNR	Bearded pig	0	0.00	Degraded	0.59	1.357409465	103.782489
Therese Lamperty*	14725	Singapore CCNR	Wild boar	69	0.47	Degraded	0.59	1.357409465	103.782489
Therese Lamperty*	6080	Singapore CCNR	Bearded pig	0	0.00	Degraded	0.59	1.356403021	103.7816176

Therese Lamperty*	6080	Singapore CCNR	Wild boar	278	4.57	Degraded	0.59	1.356403021	103.7816176
Therese Lamperty*	6080	Singapore CCNR	Pig-tailed macaque	0	0.00	Degraded	0.59	1.356403021	103.7816176
Therese Lamperty*	6080	Singapore CCNR	Long-tailed macaque	759	12.48	Degraded	0.59	1.356403021	103.7816176
Therese Lamperty*	32522	Singapore CCNR	Bearded pig	0	0.00	Degraded	0.59	1.356980966	103.7835329
Therese Lamperty*	32522	Singapore CCNR	Pig-tailed macaque	0	0.00	Degraded	0.59	1.356980966	103.7835329
Therese Lamperty*	32522	Singapore CCNR	Wild boar	107	0.33	Degraded	0.59	1.356980966	103.7835329
Therese Lamperty*	32522	Singapore CCNR	Long-tailed macaque	554	1.70	Degraded	0.59	1.356980966	103.7835329
Therese Lamperty*	2916	Singapore CCNR	Wild boar	219	7.51	Degraded	0.59	1.356934401	103.7837449
Therese Lamperty*	2916	Singapore CCNR	Long-tailed macaque	389	13.34	Degraded	0.59	1.356934401	103.7837449
Therese Lamperty*	2916	Singapore CCNR	Pig-tailed macaque	0	0.00	Degraded	0.59	1.356934401	103.7837449

Therese Lamperty*	2916	Singapore CCNR	Bearded pig	0	0.00	Degraded	0.59	1.356934401	103.7837449
Therese Lamperty*	208	Singapore CCNR	Pig-tailed macaque	0	0.00	Degraded	0.57	1.363678	103.78155
Therese Lamperty*	208	Singapore CCNR	Wild boar	44	21.15	Degraded	0.57	1.363678	103.78155
Therese Lamperty*	208	Singapore CCNR	Bearded pig	0	0.00	Degraded	0.57	1.363678	103.78155
Therese Lamperty*	208	Singapore CCNR	Long-tailed macaque	25	12.02	Degraded	0.57	1.363678	103.78155
Therese Lamperty*	5103	Singapore CCNR	Long-tailed macaque	1152	22.57	Degraded	0.61	1.378158618	103.800689
Therese Lamperty*	5103	Singapore CCNR	Pig-tailed macaque	0	0.00	Degraded	0.61	1.378158618	103.800689
Therese Lamperty*	5103	Singapore CCNR	Bearded pig	0	0.00	Degraded	0.61	1.378158618	103.800689
Therese Lamperty*	5103	Singapore CCNR	Wild boar	1199	23.50	Degraded	0.61	1.378158618	103.800689
Therese Lamperty*	4482	Singapore CCNR	Pig-tailed macaque	0	0.00	Degraded	0.64	1.366403041	103.8025915
Therese Lamperty*	4482	Singapore CCNR	Bearded pig	0	0.00	Degraded	0.64	1.366403041	103.8025915
Therese Lamperty*	4482	Singapore CCNR	Wild boar	242	5.40	Degraded	0.64	1.366403041	103.8025915

Therese Lamperty*	4482	Singapore CCNR	Long-tailed macaque	283	6.31	Degraded	0.64	1.366403041	103.8025915
Therese Lamperty*	3954	Singapore CCNR	Wild boar	117	2.96	Degraded	0.59	1.380912015	103.7973017
Therese Lamperty*	3954	Singapore CCNR	Pig-tailed macaque	0	0.00	Degraded	0.59	1.380912015	103.7973017
Therese Lamperty*	3954	Singapore CCNR	Bearded pig	0	0.00	Degraded	0.59	1.380912015	103.7973017
Therese Lamperty*	3954	Singapore CCNR	Long-tailed macaque	311	7.87	Degraded	0.59	1.380912015	103.7973017
Therese Lamperty*	18276	Singapore CCNR	Long-tailed macaque	321	1.76	Degraded	0.59	1.377491759	103.7963299
Therese Lamperty*	18276	Singapore CCNR	Pig-tailed macaque	0	0.00	Degraded	0.59	1.377491759	103.7963299
Therese Lamperty*	18276	Singapore CCNR	Bearded pig	0	0.00	Degraded	0.59	1.377491759	103.7963299
Therese Lamperty*	18276	Singapore CCNR	Wild boar	130	0.71	Degraded	0.59	1.377491759	103.7963299
Therese Lamperty*	28089	Singapore CCNR	Long-tailed macaque	3067	10.92	Degraded	0.63	1.371749245	103.8005466

Therese Lamperty*	28089	Singapore CCNR	Pig-tailed macaque	0	0.00	Degraded	0.63	1.371749245	103.8005466
Therese Lamperty*	28089	Singapore CCNR	Bearded pig	0	0.00	Degraded	0.63	1.371749245	103.8005466
Therese Lamperty*	28089	Singapore CCNR	Wild boar	2124	7.56	Degraded	0.63	1.371749245	103.8005466
Therese Lamperty*	20	Singapore CCNR	Bearded pig	0	0.00	Degraded	0.49	1.4148	103.78903
Therese Lamperty*	20	Singapore CCNR	Long-tailed macaque	0	0.00	Degraded	0.49	1.4148	103.78903
Therese Lamperty*	20	Singapore CCNR	Pig-tailed macaque	0	0.00	Degraded	0.49	1.4148	103.78903
Therese Lamperty*	20	Singapore CCNR	Wild boar	0	0.00	Degraded	0.49	1.4148	103.78903
Therese Lamperty*	3236	Singapore CCNR	Pig-tailed macaque	0	0.00	Degraded	0.57	1.378605788	103.7901796
Therese Lamperty*	3236	Singapore CCNR	Wild boar	87	2.69	Degraded	0.57	1.378605788	103.7901796
Therese Lamperty*	3236	Singapore CCNR	Bearded pig	0	0.00	Degraded	0.57	1.378605788	103.7901796
Therese Lamperty*	3236	Singapore CCNR	Long-tailed macaque	512	15.82	Degraded	0.57	1.378605788	103.7901796

Therese Lamperty*	994	Singapore CCNR	Wild boar	22	2.21	Degraded	0.57	1.378549528	103.7899386
Therese Lamperty*	994	Singapore CCNR	Long-tailed macaque	104	10.46	Degraded	0.57	1.378549528	103.7899386
Therese Lamperty*	994	Singapore CCNR	Pig-tailed macaque	0	0.00	Degraded	0.57	1.378549528	103.7899386
Therese Lamperty*	994	Singapore CCNR	Bearded pig	0	0.00	Degraded	0.57	1.378549528	103.7899386
Jedediah Brodie*	2612	Danum Valley	Long-tailed macaque	7	0.27	Intact	9.12	5.024877143	117.7304886
Jedediah Brodie*	2612	Danum Valley	Bearded pig	78	2.99	Intact	9.12	5.024877143	117.7304886
Jedediah Brodie*	2612	Danum Valley	Pig-tailed macaque	82	3.14	Intact	9.12	5.024877143	117.7304886
Luskin*	1436	Danum Valley	Long-tailed macaque	7	0.49	Intact	9.26	4.9320926	117.7753
Luskin*	1436	Danum Valley	Bearded pig	723	50.35	Intact	9.26	4.9320926	117.7753
Luskin*	1436	Danum Valley	Pig-tailed macaque	82	5.71	Intact	9.26	4.9320926	117.7753
Luskin*	2025	Danum Valley	Long-tailed macaque	7	0.35	Intact	9.26	4.932092593	117.7753048

Luskin*	2025	Danum Valley	Bearded pig	32	1.58	Intact	9.26	4.932092593	117.7753048
Luskin*	2025	Danum Valley	Pig-tailed macaque	96	4.74	Intact	9.26	4.932092593	117.7753048
Megan Baker*	563	Don Yai Wildlife Sanctuary	Wild boar	81	14.39	Intact	8.05	14.07805722	101.9644089
Megan Baker*	563	Don Yai Wildlife Sanctuary	Long-tailed macaque	0	0.00	Intact	8.05	14.07805722	101.9644089
Bill McShea*	2581	Huai Kha Khaeng Wildlife Sanctuary	Long-tailed macaque	1	0.04	Intact	9.74	15.63121111	99.21879156
Bill McShea*	2581	Huai Kha Khaeng Wildlife Sanctuary	Wild boar	1058	40.99	Intact	9.74	15.63121111	99.21879156
Jedediah Brodie*	1499	Hose mtns	Long-tailed macaque	26	1.73	Intact	7.38	2.231038889	113.6862111
Jedediah Brodie*	1499	Hose mtns	Bearded pig	196	13.08	Intact	7.38	2.231038889	113.6862111
Jedediah Brodie*	1499	Hose mtns	Pig-tailed macaque	286	19.08	Intact	7.38	2.231038889	113.6862111
Megan Baker*	3177	Huai Kha Khaeng Wildlife Sanctuary	Long-tailed macaque	17	0.54	Degraded	0.00	14.55192487	100.0234761

(Luskin, Albert, et al., 2017)	6425	Kerinci Seblat	Wild boar	1368	21.29	Degraded	4.53	–1.521746381	101.4915073
(Luskin, Albert, et al., 2017)	6425	Kerinci Seblat	Pig-tailed macaque	6889	107.22	Degraded	4.53	–1.521746381	101.4915073
(Luskin, Albert, et al., 2017)	6425	Kerinci Seblat	Long-tailed macaque	286	4.45	Degraded	4.53	–1.521746381	101.4915073
(Luskin, Albert, et al., 2017)	6425	Kerinci Seblat	Bearded pig	261	4.06	Degraded	4.53	–1.521746381	101.4915073
(Luskin, Albert, et al., 2017)	3052	Kerinci Seblat	Bearded pig	2535	83.06	Degraded	5.91	–1.645121961	101.4616761
(Luskin, Albert, et al., 2017)	3052	Kerinci Seblat	Pig-tailed macaque	752	24.64	Degraded	5.91	–1.645121961	101.4616761
(Luskin, Albert, et al., 2017)	3052	Kerinci Seblat	Long-tailed macaque	13	0.43	Degraded	5.91	–1.645121961	101.4616761
(Luskin, Albert, et al., 2017)	3052	Kerinci Seblat	Wild boar	362	11.86	Degraded	5.91	–1.645121961	101.4616761
Luskin*	4823	KhaoChong	Long-tailed macaque	0	0.00	Degraded	3.77	7.525436765	99.80452164
Luskin*	4823	KhaoChong	Wild boar	163	3.38	Degraded	3.77	7.525436765	99.80452164

Luskin*	4823	KhaoChong	Pig-tailed macaque	562	11.65	Degraded	3.77	7.525436765	99.80452164
Luskin*	4404	Khao Yai NP	Long-tailed macaque	0	0.00	Intact	8.38	14.43967262	101.3681744
Luskin*	4404	Khao Yai NP	Wild boar	267	6.06	Intact	8.38	14.43967262	101.3681744
Luskin*	2285	Lambir Hills NP	Pig-tailed macaque	252	11.03	Degraded	1.57	4.19945809	114.0209679
Luskin*	2285	Lambir Hills NP	Bearded pig	72	3.15	Degraded	1.57	4.19945809	114.0209679
Luskin*	2285	Lambir Hills NP	Long-tailed macaque	9	0.39	Degraded	1.57	4.19945809	114.0209679
(Luskin, Albert, et al., 2017)	414	Gunung Leuser	Wild boar	352	85.02	Degraded	6.76	3.765914264	98.08756989
(Luskin, Albert, et al., 2017)	414	Gunung Leuser	Long-tailed macaque	72	17.39	Degraded	6.76	3.765914264	98.08756989
(Luskin, Albert, et al., 2017)	414	Gunung Leuser	Pig-tailed macaque	178	43.00	Degraded	6.76	3.765914264	98.08756989
(Luskin, Albert, et al., 2017)	3117	Gunung Leuser	Wild boar	116	3.72	Intact	7.67	3.735748106	98.05694187

(Luskin, Albert, et al., 2017)	3117	Gunung Leuser	Long-tailed macaque	9	0.29	Intact	7.67	3.735748106	98.05694187
(Luskin, Albert, et al., 2017)	3117	Gunung Leuser	Pig-tailed macaque	718	23.03	Intact	7.67	3.735748106	98.05694187
Jedediah Brodie*	8038	Maliau	Bearded pig	2709	33.70	Intact	8.32	4.725910769	116.9341231
Jedediah Brodie*	8038	Maliau	Long-tailed macaque	6	0.07	Intact	8.32	4.725910769	116.9341231
Jedediah Brodie*	8038	Maliau	Pig-tailed macaque	631	7.85	Intact	8.32	4.725910769	116.9341231
Jedediah Brodie*	2315	Mulu	Bearded pig	95	4.10	Intact	9.33	4.099169412	114.88089
Jedediah Brodie*	2315	Mulu	Pig-tailed macaque	39	1.68	Intact	9.33	4.099169412	114.88089
Jedediah Brodie*	2315	Mulu	Long-tailed macaque	3	0.13	Intact	9.33	4.099169412	114.88089
(Takeuchi et al., 2021)	2794	Pasoh	Long-tailed macaque	24	0.86	Degraded	2.00	3.035564719	102.321165
(Takeuchi et al., 2021)	2794	Pasoh	Wild boar	669	23.94	Degraded	2.00	3.035564719	102.321165
(Takeuchi et al., 2021)	2794	Pasoh	Pig-tailed macaque	847	30.31	Degraded	2.00	3.035564719	102.321165
(Takeuchi et al., 2021)	2794	Pasoh	Bearded pig	0	0.00	Degraded	2.00	3.035564719	102.321165

(Takeuchi et al., 2021)	10534	Pasoh	Wild boar	2039	19.36	Degraded	2.01	3.034059482	102.3216491
(Takeuchi et al., 2021)	10534	Pasoh	Bearded pig	0	0.00	Degraded	2.01	3.034059482	102.3216491
(Takeuchi et al., 2021)	10534	Pasoh	Pig-tailed macaque	3018	28.65	Degraded	2.01	3.034059482	102.3216491
(Takeuchi et al., 2021)	10534	Pasoh	Long-tailed macaque	167	1.59	Degraded	2.01	3.034059482	102.3216491
(Takeuchi et al., 2021)	1661	Pasoh	Pig-tailed macaque	488	29.38	Degraded	2.07	3.031119423	102.3195
(Takeuchi et al., 2021)	1661	Pasoh	Long-tailed macaque	20	1.20	Degraded	2.07	3.031119423	102.3195
(Takeuchi et al., 2021)	1661	Pasoh	Bearded pig	0	0.00	Degraded	2.07	3.031119423	102.3195
(Takeuchi et al., 2021)	1661	Pasoh	Wild boar	244	14.69	Degraded	2.07	3.031119423	102.3195
TEAM*	1740	Pasoh	Bearded pig	0	0.00	Degraded	1.96	3.044202318	102.3194829
TEAM*	1740	Pasoh	Wild boar	533	30.63	Degraded	1.96	3.044202318	102.3194829
TEAM*	1740	Pasoh	Long-tailed macaque	31	1.78	Degraded	1.96	3.044202318	102.3194829

TEAM*	1740	Pasoh	Pig-tailed macaque	1534	88.16	Degraded	1.96	3.044202318	102.3194829
TEAM*	1710	Pasoh	Wild boar	456	26.67	Degraded	1.97	3.041791518	102.3200225
TEAM*	1710	Pasoh	Long-tailed macaque	10	0.58	Degraded	1.97	3.041791518	102.3200225
TEAM*	1710	Pasoh	Bearded pig	0	0.00	Degraded	1.97	3.041791518	102.3200225
TEAM*	1710	Pasoh	Pig-tailed macaque	854	49.94	Degraded	1.97	3.041791518	102.3200225
TEAM*	1770	Pasoh	Wild boar	674	38.08	Degraded	1.96	3.042454861	102.3206841
TEAM*	1770	Pasoh	Long-tailed macaque	24	1.36	Degraded	1.96	3.042454861	102.3206841
TEAM*	1770	Pasoh	Bearded pig	0	0.00	Degraded	1.96	3.042454861	102.3206841
TEAM*	1770	Pasoh	Pig-tailed macaque	836	47.23	Degraded	1.96	3.042454861	102.3206841
Luskin*	1175	Singapore Pulau Ubin	Bearded pig	0	0.00	Degraded	1.47	1.411504121	103.9826172

Luskin*	1175	Singapore Pulau Ubin	Wild boar	1450	123.40	Degraded	1.47	1.411504121	103.9826172
Luskin*	1175	Singapore Pulau Ubin	Long-tailed macaque	204	17.36	Degraded	1.47	1.411504121	103.9826172
Luskin*	1175	Singapore Pulau Ubin	Pig-tailed macaque	0	0.00	Degraded	1.47	1.411504121	103.9826172
Therese Lamperty*	35	Singapore Pulau Ubin	Wild boar	237	677.14	Degraded	1.42	1.407837	103.963573
Therese Lamperty*	35	Singapore Pulau Ubin	Bearded pig	0	0.00	Degraded	1.42	1.407837	103.963573
Therese Lamperty*	35	Singapore Pulau Ubin	Long-tailed macaque	6	17.14	Degraded	1.42	1.407837	103.963573
Therese Lamperty*	35	Singapore Pulau Ubin	Pig-tailed macaque	0	0.00	Degraded	1.42	1.407837	103.963573
Therese Lamperty*	5081	Singapore Pulau Ubin	Long-tailed macaque	2932	57.71	Degraded	1.44	1.407357253	103.9659955
Therese Lamperty*	5081	Singapore Pulau Ubin	Pig-tailed macaque	0	0.00	Degraded	1.44	1.407357253	103.9659955
Therese Lamperty*	5081	Singapore Pulau Ubin	Bearded pig	0	0.00	Degraded	1.44	1.407357253	103.9659955
Therese Lamperty*	5081	Singapore Pulau Ubin	Wild boar	15285	300.83	Degraded	1.44	1.407357253	103.9659955

Jedediah Brodie*	3217	Pulong Tau	Pig-tailed macaque	131	4.07	Intact	8.61	3.827728125	115.4943944
Jedediah Brodie*	3217	Pulong Tau	Long-tailed macaque	0	0.00	Intact	8.61	3.827728125	115.4943944
Jedediah Brodie*	3217	Pulong Tau	Bearded pig	254	7.90	Intact	8.61	3.827728125	115.4943944
Luskin*	1401	Singapore Sentosa S Ridges	Long-tailed macaque	0	0.00	Degraded	0.71	1.265753919	103.8104859
Luskin*	1401	Singapore Sentosa S Ridges	Pig-tailed macaque	0	0.00	Degraded	0.71	1.265753919	103.8104859
Luskin*	1401	Singapore Sentosa S Ridges	Bearded pig	0	0.00	Degraded	0.71	1.265753919	103.8104859
Luskin*	1401	Singapore Sentosa S Ridges	Wild boar	0	0.00	Degraded	0.71	1.265753919	103.8104859
Megan Baker*	1193	Ta Phraya National Park	Long-tailed macaque	0	0.00	Intact	8.70	14.13611587	102.6496376
Megan Baker*	1193	Ta Phraya National Park	Wild boar	51	4.27	Intact	8.70	14.13611587	102.6496376
Jedediah Brodie*	1410	Ulu Baram	Bearded pig	38	2.70	Intact	8.06	3.299208824	115.2227629

Jedediah Brodie*	1410	Ulu Baram	Long-tailed macaque	2	0.14	Intact	8.06	3.299208824	115.2227629
Jedediah Brodie*	1410	Ulu Baram	Pig-tailed macaque	302	21.42	Intact	8.06	3.299208824	115.2227629
(Tan et al., 2017)	4242	Ulu Muda	Long-tailed macaque	0	0.00	Intact	7.83	6.096225171	101.0022094
(Tan et al., 2017)	4242	Ulu Muda	Pig-tailed macaque	603	14.21	Intact	7.83	6.096225171	101.0022094
(Tan et al., 2017)	4242	Ulu Muda	Bearded pig	0	0.00	Intact	7.83	6.096225171	101.0022094
(Tan et al., 2017)	4242	Ulu Muda	Wild boar	926	21.83	Intact	7.83	6.096225171	101.0022094
(Tan et al., 2017)	13110	Ulu Muda	Bearded pig	0	0.00	Intact	7.83	6.101223645	101.0033197
(Tan et al., 2017)	13110	Ulu Muda	Pig-tailed macaque	2179	16.62	Intact	7.83	6.101223645	101.0033197
(Tan et al., 2017)	13110	Ulu Muda	Wild boar	4264	32.52	Intact	7.83	6.101223645	101.0033197
(Tan et al., 2017)	13110	Ulu Muda	Long-tailed macaque	0	0.00	Intact	7.83	6.101223645	101.0033197

(Tan et al., 2017)	5645	Ulu Muda	Wild boar	850	15.06	Intact	7.85	6.09942837	100.9999698
(Tan et al., 2017)	5645	Ulu Muda	Pig-tailed macaque	1251	22.16	Intact	7.85	6.09942837	100.9999698
(Tan et al., 2017)	5645	Ulu Muda	Bearded pig	0	0.00	Intact	7.85	6.09942837	100.9999698
(Tan et al., 2017)	5645	Ulu Muda	Long-tailed macaque	0	0.00	Intact	7.85	6.09942837	100.9999698
Jedediah Brodie*	1717	Ulu Padas	Long-tailed macaque	6	0.35	Intact	9.25	4.356975556	115.7126
Jedediah Brodie*	1717	Ulu Padas	Pig-tailed macaque	294	17.12	Intact	9.25	4.356975556	115.7126
Jedediah Brodie*	1717	Ulu Padas	Bearded pig	94	5.47	Intact	9.25	4.356975556	115.7126
Jedediah Brodie*	1132	Ulu Trusan	Long-tailed macaque	11	0.97	Intact	7.86	4.386916111	115.4717694
Jedediah Brodie*	1132	Ulu Trusan	Pig-tailed macaque	160	14.13	Intact	7.86	4.386916111	115.4717694
Jedediah Brodie*	1132	Ulu Trusan	Bearded pig	83	7.33	Intact	7.86	4.386916111	115.4717694

***** Unpublished data sets.

Table S5.4. Covariates used for generating species abundance estimates.

Covariate type	Covariate description	Year	Resolution	Source
Oil palm	Distance to oil palm	2015	1 m	(CRISP), National University of Singapore
Forest Integrity	Forest Landscape Integrity Index	2020	300 m	https://www.forestlandscapeintegrity.com/

Table S5.5. Linear mixed model (LMM) output for individual macaque species density estimates for Forest Landscape Integrity Index (FLII).

Species	Variable/group	Estimate	SE	df	*t* value	*p* value
Long-tailed macaque	FLII - Degraded	31.047	9.278	5.635	3.346	–
Long-tailed macaque	FLII – Intact	5	26.696	6.095	–0.976	0.366
Pig-tailed macaque	FLII - Degraded	24.109	6.7109	5.028	3.593	–
Pig-tailed macaque	FLII – Intact	14.202	0.7432	2.001	–13.331	0.005

Table S5.6. Study site characteristics for new camera trapping. MCP, maximum convex polygon.

Survey	**Annual rainfall**	**Cameras collected**	**Effort (Trap nights)**	**Duration**	**Elevation (mean ± SD)**	**Elevation range**	**MCP (km^2)**	**Camera spacing**
THAILAND								
Khao Chong / Khao Ban Tat 2018	2014.28	76	3957	2018-02-01 – 2018-04-30	524.59 ± 270.92	103 – 1234	59.01	467.95
Khao Yai 2019	1119.49	61	3553	2019-07-01 – 2019-09-25	769.64 ± 38.56	582 – 816	22.54	464.42
SUMATRA								
Gunung Leuser 2014	2828.00	69	3401	2013-12-18 – 2014-05-22	316.03 ± 250.38	25 – 888	516.15	1275.27
Kerinci Seblat 2014	2406.94	98	5356	2014-02-10 – 2014-10-04	594.03 ± 194.46	252 – 1154	813.69	1169.04
Bukit Barisan Selatan 2014	2987.80	79	5750	2014-06-15 – 2014-09-20	369.75 ± 184.97	116 – 935	473.58	1139.96

MALAYSIAN BORNEO								
Danum Valley 2019 (Sabah)	2182.68	22	1292	2019-05-24 – 2019-09-26	256.73 ± 102.02	184 – 567	8.31	520.76
Danum Valley 2018 (Sabah)	2182.85	27	1849	2018-07-12 – 2018-10-30	249.63 ± 53.23	175 – 381	15.95	614.15
Lambir Hills 2017 (Sarawak)	3078.82	67	2406	2017-05-23 – 2017-07-07	164.80 ± 65.31	60.31 – 421.44	22.06	459.95
PENINSULAR MALAYSIA								
Pasoh 2013	2081.40	58	1399	2013-05-29 – 2014-02-12	297.09 ± 160.10	98 – 674	133.53	1316.26
Pasoh 2014	2079.16	57	1314	2014-05-13 – 2014-08-01	303.14 ± 160.04	98 – 674	134.62	1321.48
Pasoh 2015	2079.78	59	1670	2015-05-07 – 2015-09-04	301.15 ± 158.15	98 – 674	134.62	1317.78
Pasoh 2016	2086.38	42	1305	2017-05-17 – 2017-08-29	308.98 ± 156.05	103 – 674	122.63	1416.43

Ulu Muda 2015a	2057.03	76	4242	2014-11-01 – 2015-01-30	278.58 ± 128.68	117 – 628	68.98	938.65
Ulu Muda 2015b	2063.01	112	4446	2015-01-31 – 2015-05-01	295.77 ± 139.83	117 – 843	113.61	731.56
Ulu Muda 2015c	2080.90	52	3582	2015-05-02 – 2015-07-31	325.38 ± 166.15	141 – 843	115.53	1227.86
Ulu Muda 2015d	2078.17	48	2862	2015-08-01 – 2015-10-30	328.92 ± 165.27	123 – 843	104.01	1237.85
Ulu Muda 2016a	2065.89	73	2220	2015-10-31 – 2016-01-29	313.62 ± 145.27	117 – 748	103.17	794.92
Ulu Muda 2016b	2054.55	60	2899	2016-01-30 – 2016-04-29	285.45 ± 135.12	117 – 628	66.96	958.39
Ulu Muda 2016c	2060.54	46	2746	2016-04-30 – 2016-07-22	301.30 ± 138.91	117 – 628	65.72	974.47
SINGAPORE								
Singapore 2019	2283.97	36	2359	2018-12-26 – 2019-03-17	41.44 ± 22.18	0 – 83	162.35	261.70

Table S5.7. N-mixture modelling of estimated abundance with 95% confidence intervals (CI) and minimum/maximum estimates for long-tailed macaque, pig-tailed macaque, wild boar and bearded pig. Variables include Forest Landscape Integrity Index (FLII) and oil palm coverage (OP).

Species	Variable	Min estimate	Min lower estimate	Min upper estimate	Max estimate	Max lower estimate	Max upper estimate	Mean percent change	Lower CI percent change	Upper CI percent change
Wild boar	OP (% 1km)	9.82	8.86	10.88	42.88	36.00	51.08	336.77	306.45	369.34
Bearded pig	OP (% 1km)	9.74	8.80	10.78	73.57	59.06	91.63	655.33	571.09	750.13
Pig-tailed macaque	OP (% 1km)	34.64	32.05	37.45	189.59	168.77	212.98	447.26	426.59	468.73
Long-tailed macaque	OP (% 1km)	1.08	0.76	1.54	99.04	70.92	138.30	9036.79	8899.76	9175.90
Wild boar	FLII	20.84	18.29	23.76	7.03	6.15	8.04	196.50	195.64	197.35
Bearded pig	FLII	5.54	4.42	6.95	25.03	21.32	29.39	–77.86	–76.34	–79.28
Pig-tailed macaque	FLII	52.74	47.81	58.18	32.37	29.52	35.50	62.94	61.98	63.90
Long-tailed macaque	FLII	7.04	4.77	10.40	1.27	0.83	1.94	456.74	437.42	476.74

Table S5.8. Linear mixed model (LMM) outputs with relative abundance index (RAI) estimates, standard errors and statistical significance in low (<1%) and high oil palm (>20%) landscapes and intact *versus* degraded forest landscapes for long-tailed macaque, pig-tailed macaque, wild boar, bearded pig, other macaque species, and all other species.

Variable/group	Estimate	SE	df	*t* value	*p* value	Species	Landscapes
FLII – Degraded	2.88	1.09	75.21	2.65	0.010	Long-tailed macaque	27
FLII – Intact	0.33	1.38	100.31	–1.84	0.068	Long-tailed macaque	31
FLII – Degraded	13.21	3.19	54.61	4.14	0.001	Pig-tailed macaque	23
FLII – Intact	7	4.41	71.36	–1.41	0.163	Pig-tailed macaque	23
FLII – Degraded	32.11	14.04	57.09	2.29	0.026	Wild boar	21
FLII – Intact	10.35	17.16	87.52	–1.27	0.208	Wild boar	22
FLII – Degraded	8.92	4.21	32	2.12	0.042	Bearded pig	9
FLII – Intact	10.46	6.14	32	0.25	0.804	Bearded pig	12
FLII – Degraded	5.56	6.51	12.39	0.85	0.409	Other macaque species	4
FLII – Intact	10.74	1.21	25.26	4.26	0.001	Other macaque species	10
FLII – Degraded	15.34	0.18	83.8	1.88	0.064	Other species	30
FLII – Intact	47.25	0.08	65.02	2.95	0.004	Other species	35
Oil palm – High	3.29	1.37	56.48	2.40	0.019	Long-tailed macaque	7
Oil palm – Low	0.70	1.48	60.15	–1.75	0.085	Long-tailed macaque	31
Oil palm – High	36.88	5.72	18.65	6.45	0.001	Pig-tailed macaque	7
Oil palm – Low	6.39	6.71	27.05	–4.55	0.001	Pig-tailed macaque	21
Oil palm – High	35.65	4.86	41.82	7.34	0.001	Wild boar	5
Oil palm – Low	6.50	5.02	55.54	–5.81	0.001	Wild boar	24
Oil palm – High	8.57	2.29	14.92	3.73	0.002	Bearded pig	4
Oil palm – Low	5.63	0.55	5.09	–5.40	0.003	Bearded pig	12

Oil palm – High	0.00	0.18	84.35	1.76	0.082	Other macaque species	0
Oil palm – Low	3.89	0.06	56.27	2.88	0.006	Other macaque species	12
Oil palm – High	10.77	0.18	84.35	1.76	0.082	Other species	7
Oil palm – Low	40.08	0.06	56.27	2.88	0.006	Other species	36

Table S5.9. Total estimated relative abundance index (RAI) and percentage dominance of pigs and macaques (combined) [see Table S5.8 for linear mixed model (LMM) estimates] in low (<1%) and high oil palm (>20%) landscapes and intact [Forest Landscape Integrity Index (FLII) 7–10] *versus* degraded (FLII 0 to <7) forest landscapes.

Variable/group	**Total RAI – pig and macaque**	**Total RAI – all other species**	**Total RAI – all species**	**Percentage dominance – pig and macaque**
Oil palm – High	84.39	10.77	95.16	88.68
Oil palm – Low	19.22	43.97	63.19	30.41
FLII – Intact	28.13	57.99	86.12	32.67
FLII – Degraded	57.12	20.90	78.03	73.21

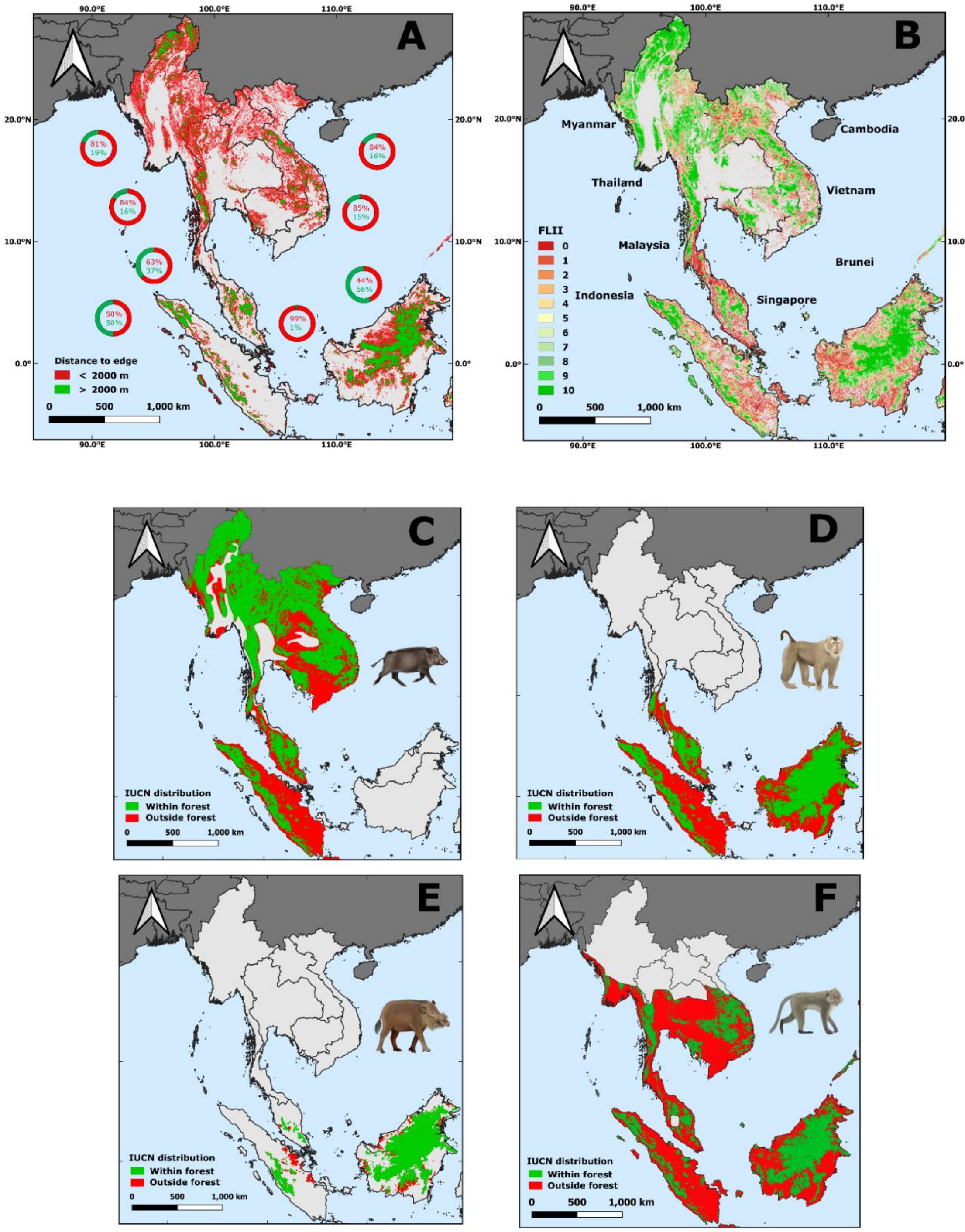


Figure S5.1. Forest distribution across Southeast Asia and showing percentage of forest within 2 km of an edge per country (A), the Forest Landscape Integrity Index (FLII) used in my analyses (B), the IUCN distribution maps within Southeast Asia, of wild boars (C), pig-tailed macaques (D), bearded pigs (E), and long-tailed macaques (F). For C–F, the species range is shown in areas within forests (green) and outside forest (red).

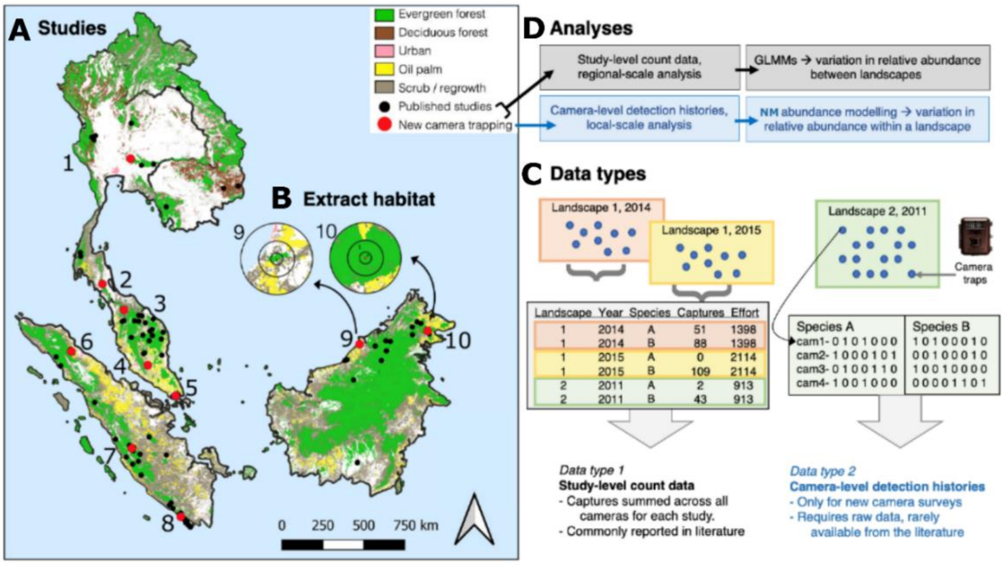


Figure S5.2. Study sites (A), schematic showing how habitat covariates were extracted in given radius around each camera or study centroid (B), description of the two types of scales of camera trap data reviewed (C), and the two analytical modelling approaches employed (D). In A, black dots represent published studies, while red dots indicate new sampling locations. Count data and habitat covariates were available for all study sites and generalized linear mixed models (GLMMs) were used to assess relationships across landscapes, where ‘landscape was the sampling unit. For new camera trapping, N-mixture models (NM) were used to assess variation in abundance within each site (D).

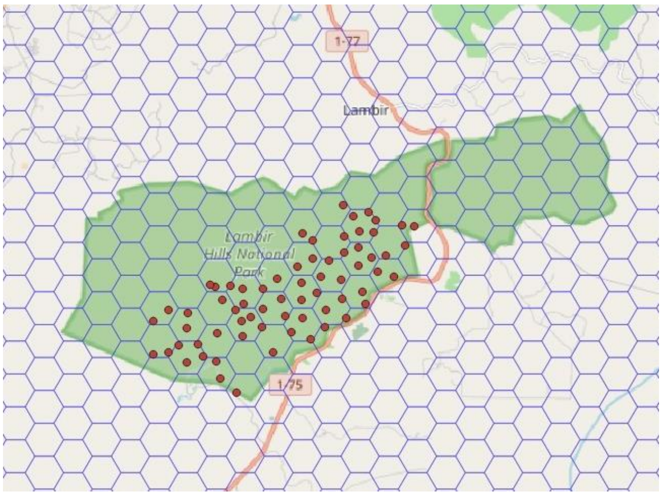
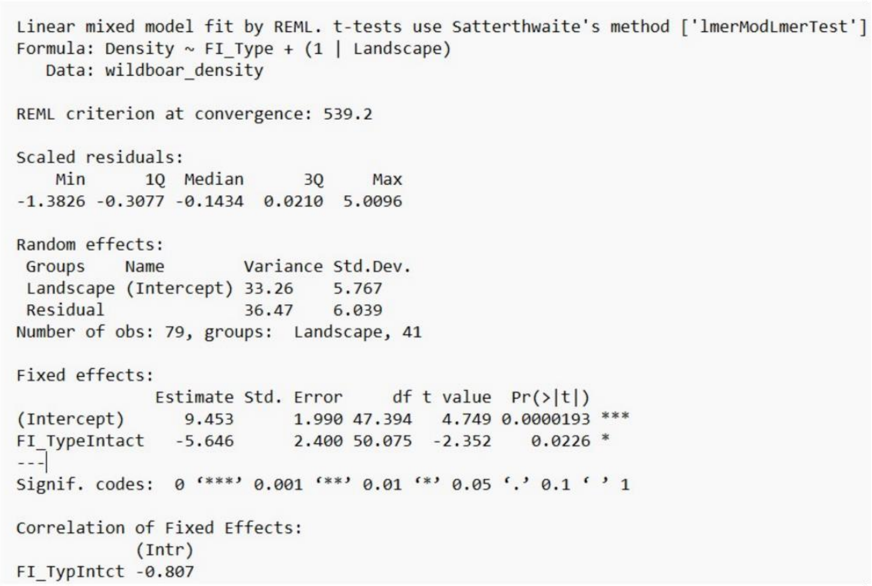


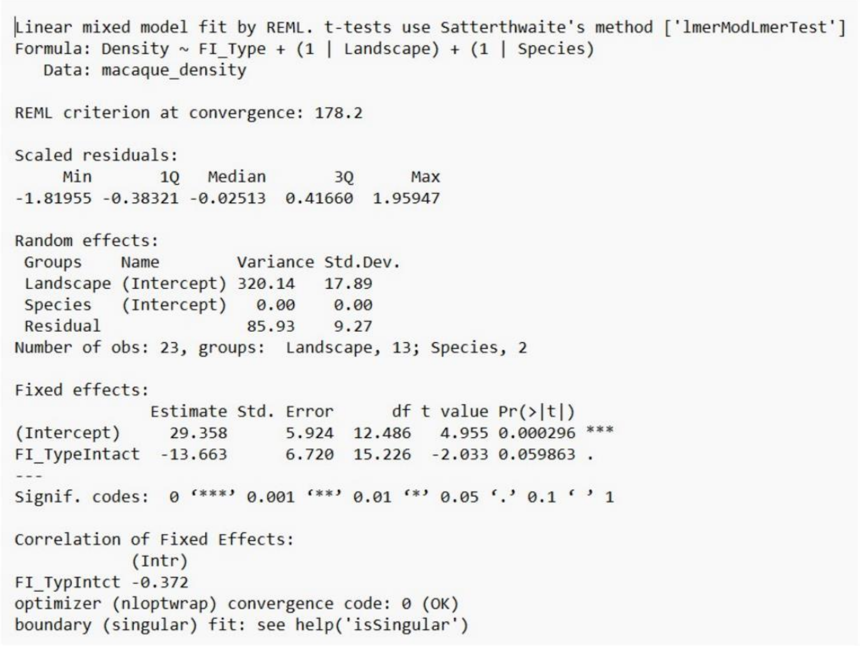
Figure S5.3. Example from Lambir Hills National Park, Malaysia showing how camera trap locations were resampled into 0.86 km^2 hexagonal grid cells used as the sampling units in the detection history matrix in the N-mixture models.

A



```
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: Density ~ FI_Type + (1 | Landscape)
   Data: wildboar_density

REML criterion at convergence: 539.2

Scaled residuals:
    Min      1Q  Median      3Q     Max
-1.3826 -0.3077 -0.1434  0.0210  5.0096

Random effects:
 Groups    Name        Variance Std.Dev.
 Landscape (Intercept) 33.26    5.767
 Residual              36.47    6.039
Number of obs: 79, groups:  Landscape, 41

Fixed effects:
              Estimate Std. Error     df t value  Pr(>|t|)
(Intercept)      9.453      1.990 47.394   4.749 0.0000193 ***
FI_TypeIntact   -5.646      2.400 50.075  -2.352    0.0226 *
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr)
FI_TypIntct -0.807
```

B



```
Linear mixed model fit by REML. t-tests use Satterthwaite's method ['lmerModLmerTest']
Formula: Density ~ FI_Type + (1 | Landscape) + (1 | Species)
   Data: macaque_density

REML criterion at convergence: 178.2

Scaled residuals:
     Min       1Q   Median       3Q      Max
-1.81955 -0.38321 -0.02513  0.41660  1.95947

Random effects:
 Groups    Name        Variance Std.Dev.
 Landscape (Intercept) 320.14   17.89
 Species   (Intercept)   0.00    0.00
 Residual               85.93    9.27
Number of obs: 23, groups:  Landscape, 13; Species, 2

Fixed effects:
              Estimate Std. Error      df t value Pr(>|t|)
(Intercept)     29.358      5.924  12.486   4.955 0.000296 ***
FI_TypeIntact  -13.663      6.720  15.226  -2.033 0.059863 .
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr)
FI_TypIntct -0.372
optimizer (nloptwrap) convergence code: 0 (OK)
boundary (singular) fit: see help('isSingular')
```

Figure S5.4. Linear mixed-effects model (LMER) outputs for (A) wild boar and (B) macaque densities in response to degraded Forest Landscape Integrity Index (FLII 0 to <7) and intact (FLII 7–10) landscapes.

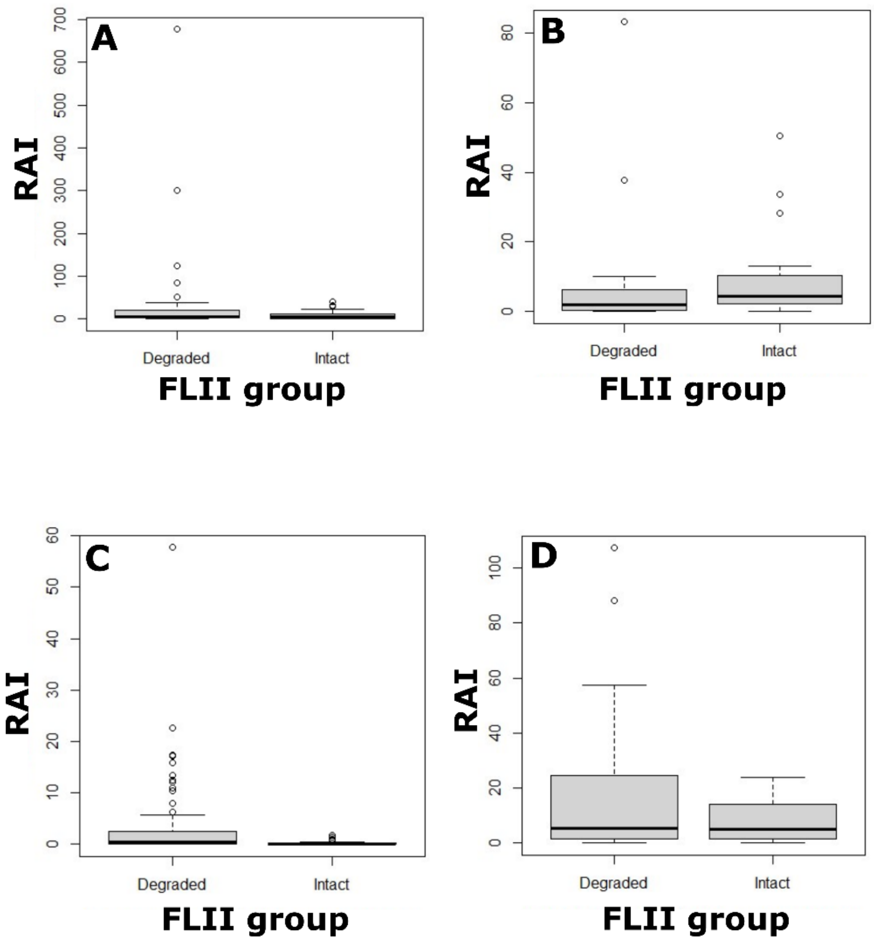


Figure S5.5. Box plots of relative abundance index (RAI) comparing between degraded [Forest Landscape Integrity Index (FLII) 0 to <7] and intact landscapes (FLII 7–10) for (A) wild boar, (B) bearded pig, (C) long-tailed macaque and (D) pig-tailed macaque.

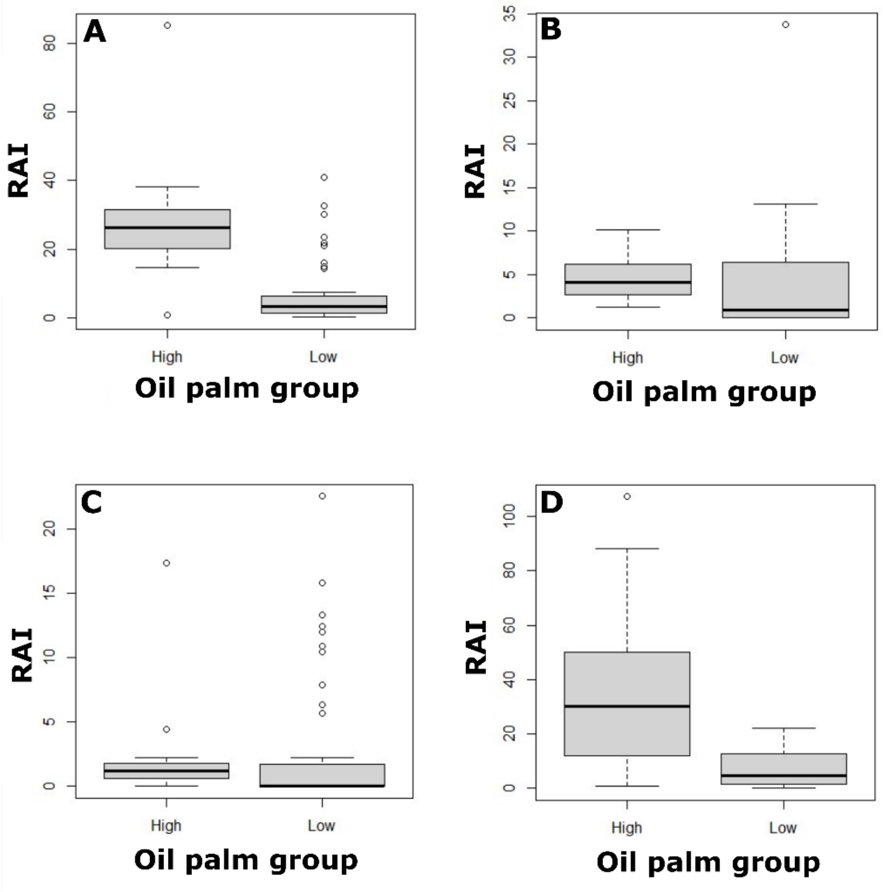
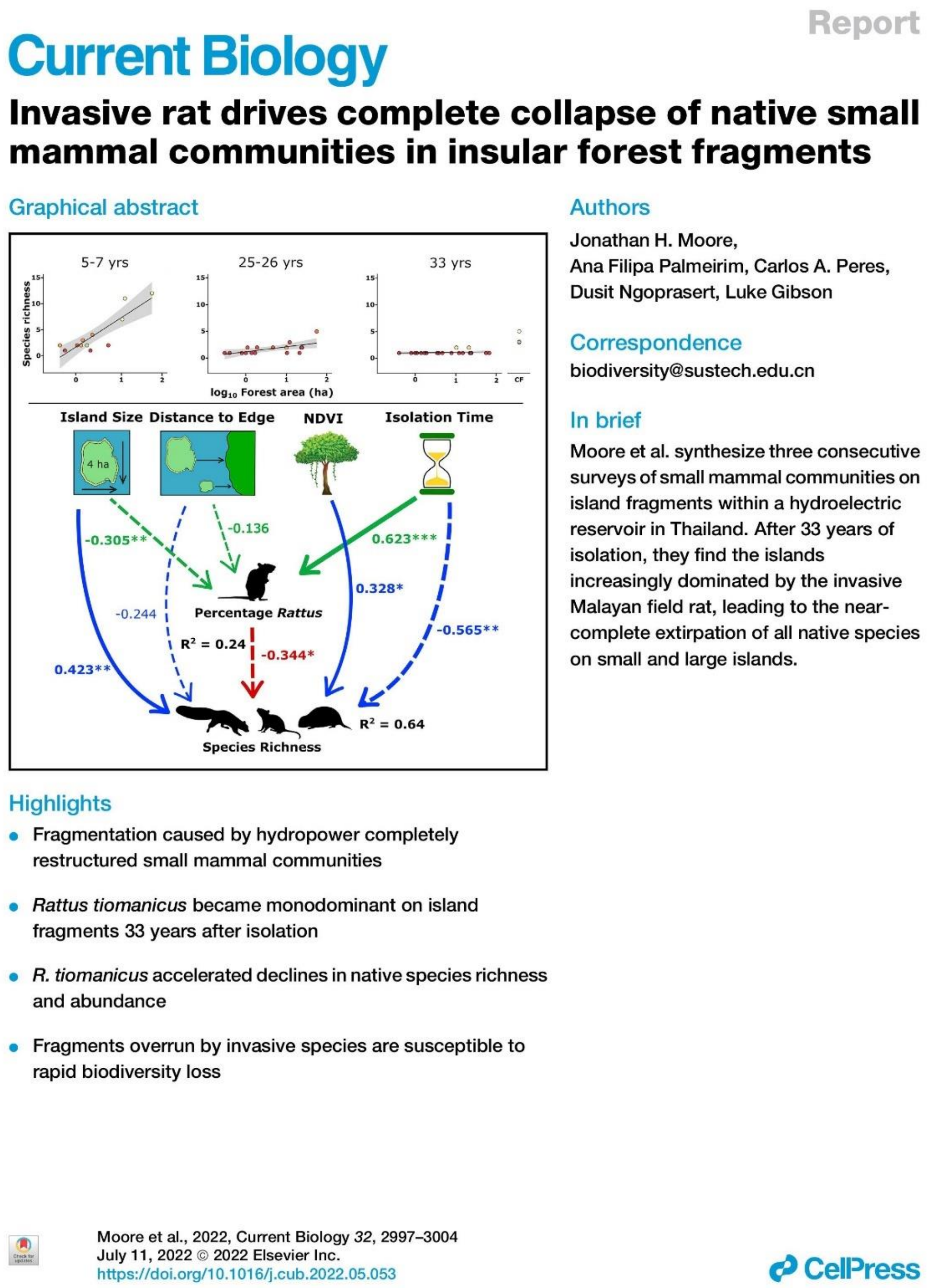


Figure S5.6. Box plots comparing relative abundance index (RAI) between landscapes with low (<1%) and high (>20%) oil palm cover for wild boar (A), bearded pig (B), long-tailed macaque (C) and pig-tailed macaque (D).

Chapter 2 Publication



Current Biology

Report

Invasive rat drives complete collapse of native small mammal communities in insular forest fragments

Graphical abstract

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In brief

Moore et al. synthesize three consecutive surveys of small mammal communities on island fragments within a hydroelectric reservoir in Thailand. After 33 years of isolation, they find the islands increasingly dominated by the invasive Malayan field rat, leading to the near-complete extirpation of all native species on small and large islands.

Highlights

- Fragmentation caused by hydropower completely restructured small mammal communities
- *Rattus tiomanicus* became monodominant on island fragments 33 years after isolation
- *R. tiomanicus* accelerated declines in native species richness and abundance
- Fragments overrun by invasive species are susceptible to rapid biodiversity loss

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CellPress

Current Biology

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Report

Invasive rat drives complete collapse of native small mammal communities in insular forest fragments

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SUMMARY

As tropical forests are becoming increasingly fragmented, understanding the magnitude and time frame of biodiversity declines is vital for 21st century sustainability goals. Over three decades, we monitored post-isolation changes in small mammal species richness and abundance within a forest landscape fragmented by the construction of a dam in Thailand.[1,2] We observed the near-complete collapse of species richness within 33 years, with no evidence of a recolonization effect across repeatedly sampled islands. Our results further revealed a decline in species richness as island size decreased and isolation time increased, accelerated by the increasing dominance of the ubiquitous Malayan field rat, *Rattus tiomanicus*. This species was already hyper-abundant on smaller islands in the initial surveys (1992–1994, 66% of individuals) but became monodominant on all islands, regardless of island size, by the most recent survey (2020, 97%). Our results suggest that insular forest fragments are highly susceptible to rapid species loss, particularly due to the competitive nature of *Rattus* accelerating the rate at which extinction debts are paid. To mitigate these impacts, reducing the extent of habitat degradation, as triggered by fragmentation and exacerbated by isolation time, can help to sustain native biodiversity while averting *Rattus* hyper-abundance.

RESULTS AND DISCUSSION

Biological assemblages isolated in forest fragments typically experience a novel hyper-disturbance regime, resulting in drastic shifts in species diversity and community composition through species extinction and turnover.[3,4] Responses to fragmentation further depend on species-specific life history traits with long-term persistence potentially favoring species with fast life histories, generalist diets, and an ability to traverse matrix habitats that separate fragments.[5] Such changes in species assemblages generally exhibit an "extinction debt" in which species experience a post-isolation relaxation period over the coming years and decades.[6,7] It is therefore important to understand the time frame and extent to which species are lost following fragmentation. However, this is challenging due to the general lack of long-term datasets following the trajectory of an animal community over multiple decades.

Here, we repeated previous work conducted in 1992–1994 and 2012–2013[1,2] focused on the same small mammal communities isolated on island fragments in Chiew Larn reservoir, a 165 km^2 hydroelectric impoundment in Thailand (Figure 1). In 2020, we conducted a third survey, completing a detailed timeline of the decline in species richness and abundance in response to fragmentation spanning 33 years (period t_1, 1992–1994 = 5–7 years; t_2, 2012–2013 = 25–26 years; t_3, 2020 = 33 years post-isolation). For all surveys combined, raw captures amounted to 1,789 small mammal individuals representing 12 species. We used these data to quantify the rate at which native small mammal species richness and abundance changed over time, to quantify the rate at which hyper-abundance of a generalist rodent increased over time, and to identify the primary drivers impacting the trajectory of small mammal richness and abundance using path analysis. Finally, we discuss the implications of the results in the context of the equilibrium theory of island biogeography (ETIB) and the rate at which "extinction debts" are paid.[6,7]

Native small mammal richness declines over 33 years of isolation

As most species residing within biodiverse tropical forests are forest specialists, they often suffer disproportionate declines or even extinction when exposed to human modified landscapes;

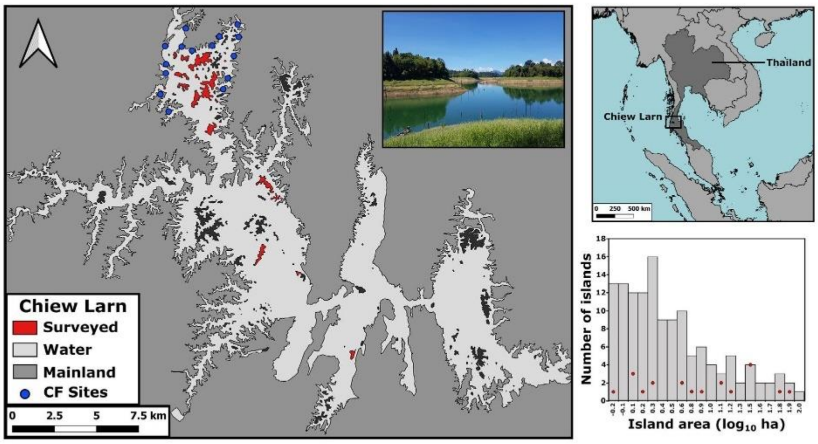

Figure 1. Map of study site

Chiew Larn reservoir flooded 165 km^2 of forest habitat in Surat Thani Province, Thailand (9°07′35.9″N, 98°37′24.2″E), creating over 100 islands in the process. Surveyed islands are indicated in red, and the overall island size distribution is shown at bottom right (red points indicating surveyed islands). See also Figure S1 for the estimated proportion of *R. tiomanicus* in small mammal communities across all islands.

the declines of these species are mediated by competitively inferior functional traits including small body size, reduced aggression, limited mobility, dietary specialization, and habitat specialization.[8–11]

Our 33-year dataset supports these negative trends showing a dramatic decrease in the total (and average ± SD) number of species on islands, from 12 (4.08 ± 3.82) to 6 (1.75 ± 1.06) to 3 (1.10 ± 0.31), in t_1, t_2, and t_3, respectively. Mainland continuous forest (CF) richness in t_3, with 6 (3.30 ± 0.47) species, was twice as high as islands in t_3 but 50% lower than the species richness observed in t_1. Species-area relationships (SARs) over sequential sampling periods revealed a strong positive effect of island area in t_1 ($t = 5.63$, $p < 0.001$), a marginal effect in t_2 ($t = 2.93$, $p < 0.01$) and no effect in t_3 ($t = 0.94$, $p > 0.05$), demonstrating the complete collapse of the SAR due to the monodominance of *Rattus tiomanicus* (Figure 2; Table S1). Additionally, two squirrel and one treeshrew species had been detected in t_1 and t_2, whereas no such species were detected by t_3.

The primary traits likely accounting for these species' declines are aggression and body size, as larger and more aggressive species are generally competitively superior to smaller and subordinate species.[12] For example, in New Zealand, the larger brown rat *Rattus norvegicus* outcompetes the smaller black rat *Rattus* through direct conflict,[13] whereas the black rat in turn is able to directly outcompete the smaller Polynesian rat *Rattus exulans*.[14] Additional traits potentially contributing to species declines might include narrow niche breadths,[15] whereby dietary and habitat specialists are at higher risk of extinction[16–18] and predisposed to limited dispersal capabilities that prevents recolonization from source populations.[11,19] It is possible that the observed reduction in richness within CF sites compared with t_1 is due to a combination of edge effects and increasing habitat degradation, paralleling some of the conditions present on islands, thereby decreasing native species richness while allowing *Rattus* dominance to increase.

Crucially, we found that the extent and rate at which species richness declined on Chiew Larn islands far exceeded that of other community-wide small mammal studies worldwide within island fragments. We compiled analogous studies from a global review on extinction debts[20] along with additional literature searches[21,22] and found that no previous study had demonstrated the complete dominance by a single species, as seen at Chiew Larn. In fact, our 2020 results revealed a collapse of species richness 7 years faster than the theoretical prediction of complete relaxation to monodominance that was derived from the same study landscape.[2]

Changes in native small mammal and *Rattus tiomanicus* abundance over 33 years of isolation

As with species richness, abundance of forest specialists is also expected to decline in response to unfavorable changes in vegetation structure induced by edge effects,[23] whereas abundance of generalist species may increase.[5] One such generalist species detected in t_1 was *R. tiomanicus*. Although Chiew Larn is technically within the native range of *R. tiomanicus*,[24] in this context, the species is behaviorally characterized as invasive. Its habitat preferences include urban areas, selectively logged forest, oil palm plantations, and other areas of intermediate land-use intensity,[25–27] whereas the original vegetation found in Chiew Larn prior to insularization was primary, undisturbed lowland evergreen forest. This renders *R. tiomanicus* as a prime beneficiary of the post-isolation conditions at Chiew Larn.

Over 33 years, we observed a slight increase in the average small mammal abundance per island over time, which became

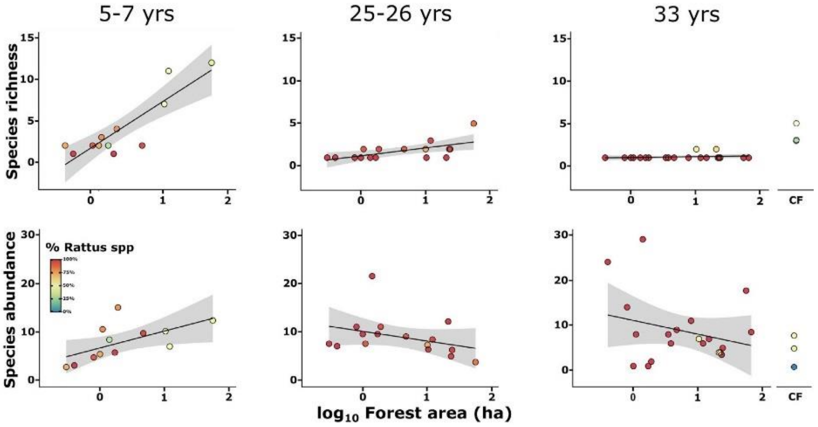

Figure 2. Changes in small mammal species richness and abundance in relation to island area over time

Species richness (top) and overall abundance (bottom) versus island area (log$_{10}$) over time, 5–7 years (t_1), 25–26 years (t_2), and 33 years (t_3) post-isolation (see Table S1 for model outputs). Each point represents one island fragment with three mainland continuous forest (CF) control sites in the final survey; points are color-coded according to the percentage of all individuals represented by *Rattus tiomanicus*. Regression lines (black) with 95% confidence intervals (gray) are highlighted. See also Figure S2 for a version of Figure 2 using only data for the 12 islands that were resampled over all three time periods.

progressively dominated by the hyper-abundant *R. tiomanicus*, increasing from 7.95 ± 3.80 individuals (t_1) to 8.85 ± 7.36 individuals (t_3). The 2020 mainland CF average abundance (6.00 ± 3.41 individuals) was lower than that on islands (Figure 2). Focusing on *R. tiomanicus* only, we saw a 62% increase in average abundance per island from t_1 (5.33 ± 3.07 individuals) to t_3 (8.56 ± 7.49 individuals), which was 3.4 times higher than CF average abundance in t_3 (2.47 ± 2.50 individuals). Abundance was standardized to number of individuals per transect by dividing total abundance by the overall sampling effort (number of transects) per island per year.

Overall, the most abundant non-*Rattus* species in t_1 were the arboreal Indomalayan pencil-tailed tree mouse *Chiropodomys gliroides* (n = 11.5, 12.1% of the records) and the common treeshrew *Tupaia glis* (n = 5, 5.4%); combined, native species amounted to 34.0% of the captures in t_1. The proportional abundance of non-*Rattus* species on islands declined to 4.2% and 3.4% by t_2 and t_3, respectively, and neither squirrels nor treeshrews were detected by t_3. Over the sequential sampling periods, we report a significant positive relationship between species abundance and island area in t_1 (t = 2.704, p = 0.022). However, no such relationship was found for t_2 or t_3, although there was a trend toward higher abundance on smaller islands (t = −1.341, p = 0.196) as driven by *R. tiomanicus* dominance (Figure 2; Table S1). In fact, in contrast to other species, *R. tiomanicus* was the most abundant species during all survey periods and increased in proportional abundance over time: from 66.0% (t_1) to 96.6% (t_3). This species initially became hyper-abundant on smaller islands in t_1, before reaching monodominance on all islands, regardless of size, by 2020 (Figure S1). A model averaging approach predicting the percentage of *R. tiomanicus* across all survey periods revealed a negative relationship with island size (log$_{10}$) (z = 2.369, p = 0.018) and a positive relationship with time since isolation (z = 4.438, p < 0.001) (Tables S2 and S3).

R. tiomanicus became monodominant throughout the entire landscape, whereas other native species populations crashed. Initially, in t_1, the two most arboreal species were best able to escape *Rattus* dominance, whereas more terrestrial species declined rapidly likely due to more intense competition with *Rattus*. However, over time, these arboreal species eventually disappeared, likely due to sustained competition with *Rattus* combined with their highly limited aquatic dispersal abilities,[19] which prevented further recolonization from source populations. *Rattus* spp. only require a small number of founder individuals to establish an insular population and can breed year-round depending on resource constraints or density-dependent effects.[28] It is possible that as islands became more degraded over time from edge effects, pioneer plant species such as bamboo increased, potentially providing additional nesting sites. Bamboo fruiting has also been linked to population irruptions in *Rattus* spp.[29] *Rattus* spp. also bear many traits ideal for exploiting increasingly degraded habitats, for example, using highly opportunistic foraging strategies, with broad diets consisting primarily of plant material, insects, and terrestrial crustaceans;[30] furthermore, the overlap in dietary requirements with co-occurring species such as murid rodents and tupaiids could have contributed toward their declines.[31] Although *Rattus* spp. behave as ground and understorey habitat generalists, they are highly adept climbers that indiscriminately use the three-dimensional forest structure,[32] unlike native species whose movement patterns are negatively impacted by altered forest structure.[33–35] Similar to other murid rodents, *Rattus* spp. also exhibit high dispersal capacity in traversing the inhospitable

Table 1. Structural equation models examining direct and indirect effects on small mammal species richness and abundance

Model	*C*	p	df	AICc
Species richness (n= 48)				
Direct[a]	54.071	0	4	545.509
Indirect[a]	18.849	0.004	6	557.693
Direct and indirect	3.42	0.181	2	541.726
Species abundance (n= 48)				
Direct[a]	118.153	0	4	828.664
Indirect[a]	18.157	0.006	6	668.910
Direct and indirect	3.420	0.181	2	669.952

SEM best-fit criteria for direct and indirect effects on species richness and abundance. With Fisher's test *C*, p value, and AIC_c. (Lowest AIC_c number indicates the best fit model, given that piecewise SEM assumptions are met.)

Notes: SEMs built to identify the primary candidate model predicting species richness (n = 12, 16, and 20 islands in t_1, t_2, and t_3, respectively) and species abundance (n = 12, 16, and 20 islands) over the three sampling periods. SEMs were split into direct effects (island area, NDVI, distance to mainland, years isolated), indirect effects (% *Rattus* dominance), and combining both direct and indirect effects. All SEMs were fitted with Poisson distribution. *C* stats, p values, and degrees freedom (df) relate to Fisher's test, which is used to determine if there are non-random associations between variables. The Akaike information criterion adjusted for small sample sizes (AIC_c) was used to measure model fit; the lowest AIC_c number indicates the best fit model, given that piecewise SEM assumptions are met.

[a] Indicates piecewise SEM assumptions not met for the model from Fisher's test

open-water matrix.[36,37] We recorded 10 events of *R. tiomanicus* traversing between transects (separated by a minimum distance of 500 m), with one 860-m dispersal event swimming between different islands and a second >1.7-km event swimming from an island to a mainland CF transect. We also directly observed three separate events of *R. tiomanicus* actively swimming between islands (J.H.M., unpublished data). This proficient dispersal ability likely contributed to *Rattus* population expansion ensuring island colonization and migration during times of food shortage to relieve density-dependent effects. Alongside several additional factors such as aggressiveness, size-mediated dominance, loss of native predators, and increased habitat degradation on island fragments, these traits helped to ensure that *R. tiomanicus* became ubiquitous throughout the Chiew Larn archipelago.

Native species richness and abundance responses to *Rattus* hyper-abundance

As the population dynamics of co-occurring species followed a very similar chronosequence in response to the *Rattus* proliferation across islands, it is difficult to disentangle cause and effect. We therefore used piecewise structural equation modeling (SEM)[38] to understand the importance of *R. tiomanicus* as an indirect driver of small mammal species richness and abundance decline, which we compared with direct environmental effects, including island size, distance to mainland, normalized difference vegetation index (NDVI), and isolation time. SEM analysis demonstrated that the primary drivers of altered local species richness were a combination of direct environmental effects, including a positive relationship with island area and NDVI and a negative relationship with isolation time, and indirect effects, including a negative effect of the magnitude of *R. tiomanicus* dominance (Table 1; Figure 3). Increasing *R. tiomanicus* dominance was best explained by environmental effects, with a negative relationship with island area and a positive relationship with isolation time. The direct effect of distance to mainland on species richness and *R. tiomanicus* abundance was not significant (Figure 3). SEM analysis revealed that the primary predictors of species abundance declines were a combination of a direct environmental effect, a negative relationship with distance to mainland, and a strong negative relationship with *R. tiomanicus* dominance (Table 1; Figure 3). The direct environmental effects of island area, NDVI and isolation time, had no significant effect on species abundance.

Invasion ecology considers the mechanisms facilitating the establishment, spread, and subsequent impacts of a non-native species.[39] Our results indicate that densities of *R. tiomanicus* were initially highest on smaller islands, which were predominantly more degraded, then subsequently increased on larger islands as the habitat structure there also degraded over time. *R. tiomanicus* therefore benefited from the changing habitat conditions that ultimately contributed to the suppression of other native species. There are three main potential forms of competition between *R. tiomanicus* and other native species that could explain our results. The primary form likely explaining most observed trends is "interference competition," in which direct agonistic interactions between native and invasive species can prevent access to common resources and territories resulting in declines and ultimately extinction of native species.[40] Interference competition has often been observed between *Rattus* spp. and native rodents,[26,41] with dominance through direct physical contest and aggression often favoring larger-bodied species.[12] This may in part explain the continued, although declining, presence of Müller's rat *Sundamys muelleri* detected on two Chiew Larn islands in 2020, down from 6 islands in 1994, whereas all other smaller bodied species had been extirpated.

A second form of competition known as "exploitation competition" may also be contributing to the observed results, in which native species are indirectly negatively affected by an invasive species through competition for common resources such as food and nesting sites. Previous work on the dietary composition of rodents within an artificial island archipelago demonstrated that interspecific dietary overlap increases on islands, leading to more intense competition for resources between species.[42] This is likely due to changes in available resources on islands, as mean seed sizes have been found to decline on smaller island fragments.[43] As *Rattus* spp. are proficient climbers that can utilize all levels of forest strata,[32,41] this mobility allows them to indirectly outcompete native species whose movements are often inhibited by increasingly degraded landscapes[34,35] limiting their access to food resources and nesting sites. However, as no direct behavioral interactions were recorded during the 33-year dataset, no definitive assessment can be made regarding whether *Rattus* is outcompeting native species through either "interference" or "exploitation" competition.

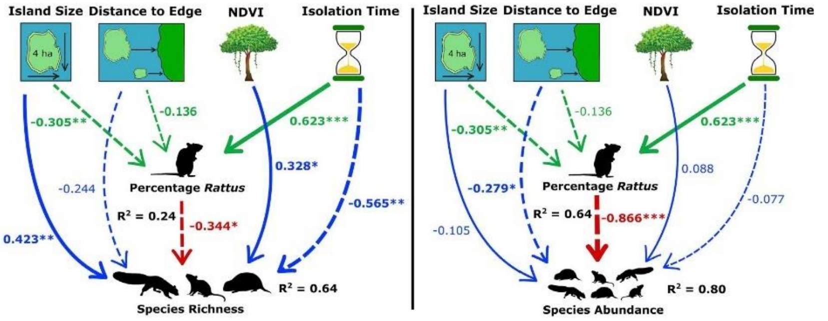

Figure 3. Structural equation models examining environmental effects and *R. tiomanicus* abundance on small mammal species richness and abundance

"Best" structural equation models (SEMs) predicting species richness (12, 16, and 20 islands in t_1, t_2, and t_3, respectively) and abundance (12, 16, and 20 islands) across three time periods with direct environmental effects, including island size (ha), distance to mainland (m), normalized difference vegetation index (NDVI), and isolation time, and indirect effects, percentage of *Rattus tiomanicus*. Standardized coefficients are presented for each relationship, with solid and dashed lines indicating positive and negative relationships, respectively. Dark blue lines indicate direct environmental effects on richness; green lines indicate direct environmental effects on % *Rattus* dominance, and the red line indicates direct effects of *R. tiomanicus* abundance on overall species richness and abundance. Asterisks indicate the level of significance for relationships (*$p < 0.05$, **$p < 0.01$, ***$p < 0.001$) with a coefficient of determination (R^2) for each response variable. Line thickness is scaled to represent relative strength of effects.

A third form of competition possibly contributing to some of the observed trends is "apparent competition," which occurs when native mesopredator abundance increases due to a prey surplus, indirectly suppressing native species through elevated predation levels.[44,45] *Rattus* may be supplementing that prey surplus but continue to dominate the landscape due to their rapid reproductive capacity, whereas other native species decline.[28] An alternative explanation for increases in mesopredator abundance is "mesopredator release," which occurs when apex predators, which normally regulate mesopredator populations, decline due to fragmentation effects.[46–48] Contrastingly, the "predator mediated co-existence hypothesis" suggests that predators are critical in maintaining prey diversity by controlling highly competitive species within the community; consequently, when predators are lost due to fragmentation, prey diversity may decline as hypercompetitive generalist species take over.[49,50] To address these three theories surrounding mesopredator abundance, we evaluated data from 27 camera traps on islands, amounting to 1,159 trap nights and >28,800 photos. We detected two mammalian mesopredators on islands, four independent captures of the golden cat *Catopuma temminckii* with a relative abundance index (RAI) of 0.34 and one capture of the common palm civet *Paradoxurus hermaphroditus* with an RAI of 0.07. Independent captures are defined as images taken more than 30 min apart, whereas RAI is defined as the number of independent captures per 100 trap nights.[51] In comparison, work performed within the mainland of the Khlong Saeng—Khao Sok Forest Complex[52] found the RAI of golden cats to be 3× higher at 1.08, whereas common palm civets had a similar RAI at 0.09. In addition, of the nine mesopredator species detected in the mainland forest study, only two were detected on islands suggesting that mesopredators are limited within insular areas potentially contributing to *Rattus* proliferation.

Implications for ETIB and extinction debt

Despite a lack of clarity of the key mechanisms driving the full establishment and consequential dominance of *R. tiomanicus* populations across the Chiew Larn archipelago over three decades, their proliferation represents a departure from the main tenets of island biogeography theory,[53,54] which expresses a simpler equilibrium of species richness balanced by a combination of local extinctions and immigration of new species. *Rattus* hyper-abundance also accelerated the rate at which "extinction debts" were paid. Our results indicate that *R. tiomanicus* has a strong detrimental effect on small mammal species richness to the point of neutralizing the SAR (Figures 2 and 3), with *Rattus* monodominance elevating local competitive conditions and subsequently preventing the re-establishment of local species from source populations. Examples of *Rattus* impacting ETIB and "extinction debts" are limited within the literature, and consequently, our results here provide important insights into how *Rattus* spp. can decimate faunal assemblages in insular fragmented forest habitats, serving as a warning to other landscapes that are yet to experience a *Rattus* invasion.

Implications to conservation management

The hyper-abundance of an invasive rodent in insular fragmented forest landscapes threatens not only the diversity of small mammals but also that of birds,[20] reptiles,[55] invertebrates,[56] and plants.[57] These taxa have all been documented as impacted by *Rattus* spp. invasions on true islands,[28,58] and on insular forest fragments could also suffer shifts in community structure as part of an ecosystem-wide ecological meltdown.[59] Local human communities may also be affected by elevated abundances of *R. tiomanicus*, which are potential vectors for diseases such as leptospirosis,[60] and through economic damage caused by crop raiding.[61]

The key management recommendation to suppress *Rattus* populations would be to prevent landscape fragmentation in the first place as these rodents are human-commensals and are less likely to proliferate within large tracts of undisturbed primary forest.[25–27] Previous studies in other archipelagic landscapes also suggest that retaining forest patches larger than 475 ha can support species-rich vertebrate communities containing $\geq$80% of the local fauna.[62] Maintaining >40% forest cover at the landscape scale and a high-quality matrix between patches would further ensure a nearly full complement of species.[63,64] Direct control or eradication of invasive *Rattus* populations using techniques such as poisoning (anticoagulants) and trapping[65] has been attempted but often fails due to the "sink effect" with rapid reinvasions from wider meta-populations.[36,66]

CONCLUSIONS

Our results suggest that *Rattus* hyper-abundance in fragmented insular landscapes could be playing a role in accelerating the rate at which species are lost, faster than that expected by the ETIB alone. Once *Rattus* secures a foothold, local competitive conditions simply become too hostile for native populations to become re-established. We found that virtually the entire native small mammal fauna can be lost in a tropical archipelagic landscape within three decades, illustrating the short time frame at which an extinction debt can be paid in extreme conditions. Although this study is limited in identifying the primary mechanisms leading to *Rattus* monodominance, the potent combination of favorable species traits such as increased aggressiveness, larger body size, and high dispersal capacity, alongside elevated habitat degradation and reductions in native predators on island fragments, all likely contributed to its proliferation throughout the landscape. This study indicates that small mammal assemblages are likely to vanish from other small island fragments (<100 ha), especially those overrun by invasive species and experiencing limited connectivity demonstrating the devastating effects of dam construction on native fauna. This also forewarns the potential for *Rattus* invasions throughout other insular fragmented landscapes both in Southeast Asia, Africa, and the Neotropics, as native species' impacts on co-occurring species can be a good predictor of future invasiveness outside their native range.[5,65] Conservation efforts should focus on retaining and restoring large tracts of continuous forest landscapes to maintain stable and ecologically balanced faunal assemblages.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- RESOURCE AVAILABILITY
    - ○ Lead contact
    - ○ Materials availability
    - ○ Data and code availability
- EXPERIMENTAL MODEL AND SUBJECT DETAILS
    - ○ Ethics statement
    - ○ Study site
- METHOD DETAILS
    - ○ Small mammal surveys
    - ○ Environmental and biological variables
- QUANTIFICATION AND STATISTICAL ANALYSIS
    - ○ Data analysis

SUPPLEMENTAL INFORMATION

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AUTHOR CONTRIBUTIONS

J.H.M., A.F.P., C.A.P., and L.G. designed the study. J.H.M., A.F.P., and L.G. conducted surveys. J.H.M. and A.F.P. analyzed the data. D.N. provided logistical support. J.H.M. wrote the first draft of the manuscript, and all authors contributed to the revision of the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Software and algorithms		
R Statistical Software	R Project	https://www.r-project.org
Contributed R packages	Comprehensive R Archive Network (CRAN)	https://cran.r-project.org
R code	figshare	https://doi.org/10.6084/m9.figshare.19803922

RESOURCE AVAILABILITY

Lead contact

Further information and requests should be directed to and will be fulfilled by the lead contact, Luke Gibson (biodiversity@sustech.edu.cn).

Materials availability

The study did not generate new unique reagents.

Data and code availability

- All data reported in this paper will be shared by the lead contact upon request.
- All original code has been deposited at figshare and is publicly available as of the date of publication. DOIs are listed in the key resources table.
- Any additional information required to reanalyze the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Ethics statement

All surveys in this study were carried out in accordance with regulations on animal ethics and other laws and approved by the National Research Council of Thailand (No. 0402/4356).

Study site

This study was conducted at Chiew Larn reservoir in Surat Thani province, Thailand (9°07’35.9"N, 98°37’24.2"E) (Figure 1). The landscape consists of lowland monsoon evergreen forest with a mosaic of successional stages, exposed to a mean annual rainfall of 2,365 mm and mean annual temperatures of 26.8°C. The impoundment reservoir flooded 165 km^2 of forest following construction of Rajjaprabha Dam, completed in 1987. In the process, more than 100 islands were formed within the reservoir, ranging in size from <1 to >100 ha (mean size ≈ 8 ha). The forest surrounding the reservoir is divided between two major protected areas, including Khlong Saeng Wildlife Sanctuary, originally established in 1974 and covering 1,155 km^2. This forest served as a useful continuous forest control site.

METHOD DETAILS

Small mammal surveys

We surveyed small mammal assemblages during three sampling periods: 12 islands from t_1 (3 surveys), 16 islands (12 resampled from t_1) from t_2 (2 surveys), and 20 islands (15 resampled from t_2, 12 resampled from t_1) in t_3 (1 survey). Island sizes ranged from 0.3 to 63 ha. Abundance was standardized to number of individuals per single transect by dividing total abundance by the sampling effort (number of transects) per island per year. Small terrestrial mammals were surveyed using a combination of Sherman (10 x 8 x 30.5 cm) and Tomahawk (14 x 14 x 41 cm) live traps arranged along transects. The number of transects per island was proportional to island area,[67] with one transect on islands <20 ha, two transects on islands 20-40 ha, and 3 transects on islands >50 ha. We also surveyed three continuous forest (CF) sites, deploying 5 transects at each site >500 m from the reservoir edge. Each transect consisted of 10 trap-stations, each station separated by 15 m. At each station, we placed one Tomahawk trap on the ground and one Sherman trap within the understory vegetation, attached to lianas or tree trunks, to sample both terrestrial and arboreal species. Traps were baited using a combination of bananas, oats and peanut butter, and monitored for 5 consecutive nights, checked and re-baited every 24 hours. Captured individuals were identified using,[68] sexed and measured for body weight, body length, and tail length. All field methods in the most recent surveys were consistent with previous surveys.[1,2] All animals captured in this study were marked using ear tags and released unharmed following the guidelines of the American Society of Mammologists.[69]

Environmental and biological variables

The following environmental variables were examined to test their effect on the diversity of the small mammal assemblage persisting within the fragmented landscape: island area ($\log_{10}$ x), shape index calculated as (Perimeter / (2 * SquareRoot(PI * Area)) and island perimeter length, distance to mainland, isolation time (yrs), and Normalized Difference Vegetation Index (NDVI). The % dominance of *Rattus tiomanicus* was also included as a covariate. Variance inflation factor (VIF) values were generated to indicate whether variables contained high collinearity, with an ideal value <2; we also checked for variable inter-correlation. This resulted in the exclusion of shape index and island perimeter length (Figure S2). All mapping and GIS layer manipulation was performed using QGIS version 3.16.4.[70] Island sizes and distance to mainland were extracted using open street map data.[71] NDVI was generated as an assessment of habitat quality, calculated using the QGIS raster calculator, by first subtracting the red band values from the near-infrared (NIR) bands, and then dividing this value by the sum of the red and NIR bands. Reflectance bands were extracted from Landsat 8 imagery.

QUANTIFICATION AND STATISTICAL ANALYSIS

Data analysis

Data analysis was conducted using R,[72] including the packages “Cairo”, “ggplot2”, “corrplot”, and “HH”. Generalized Linear Models (GLMs) were used to examine the patterns of species persistence over time, using island area ($\log_{10}$) per survey period to predict species richness and abundance. Data from 1992-94 and 2012-2013 were modeled separately focusing on island size and proportional *Rattus tiomanicus* abundance as primary predictors of species richness. Species richness data from 2020 was extremely low for all islands, due to the monodominance of *R. tiomanicus*, so analysis could not be performed. The relationship between island size and proportional *R. tiomanicus* abundance was estimated using linear models for each year and projected to all unsurveyed islands to depict the increasing dominance of *R. tiomanicus* over time (see Figure S1; Table S2).

We then used piecewise Structural Equation Modeling (SEM) to disentangle the direct environmental effects from the indirect effects as mediated by *R. tiomanicus* driving small mammal species richness and abundance. The piecewiseSEM R package was used to generate SEMs.[73] Piecewise SEMs are a form of path analysis which test causal relationships between dependent and response variables.[38] This allows for testing and quantifying indirect effects that can be missed by any single model.[74] Path diagrams were converted into a set of linear equations, which were evaluated separately, allowing for smaller sample sizes to be analyzed.[73] Three path diagrams were designed to represent direct, indirect and a combination of direct and indirect effects combined on either native species richness or abundance; these were then compiled into three SEMs, which consisted of one Generalized Linear Mixed Model (GLMM) with either only direct (environmental) or indirect (% *R. tiomanicus*) variables or a combination of the two and a comparable GLMM. “Island” identity was included as a random effect to account for the 20 different islands sampled during t_1, t_2 and t_3.

The goodness-of-fit for the SEMs was assessed using Shipley’s test of direct separation, determining if there are any missing relationships among unconnected variables.[38] The basis set constitutes a set of all potential relationships among unconnected variables in a path diagram (i.e. conditional independence). Shipley’s test is performed by combining all p values for the basis set to produce a test statistic, Fisher’s C. To avoid a saturated model which would prevent assessment of the goodness-of-fit, NDVI provided the smallest effect and was removed from the *R. tiomanicus* dominance linear model to prevent model saturation when running SEM analysis. An Akaike’s information criterion value adjusted to small sample sizes (AIC_c) was also obtained using the Fisher’s C statistic,[75] and we ordered each of our three SEMs (direct, indirect, and both) based on AIC_c values to evaluate model fit, the lowest AIC_c number indicating the best fit model, given that piecewise SEM assumptions are met. Models with ΔAIC_c values <3 were defined as providing substantial support, >3 and <7 were considered as moderately supportive, and >10 providing little to no support relative to the model set.

Chapter 5 Publication

BIOLOGICAL
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The rise of hyperabundant native generalists threatens both humans and nature

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ABSTRACT

In many disturbed terrestrial landscapes, a subset of native generalist vertebrates thrives. The population trends of these disturbance-tolerant species may be driven by multiple factors, including habitat preferences, foraging opportunities (including crop raiding or human refuse), lower mortality when their predators are persecuted (the 'human shield' effect) and reduced competition due to declines of disturbance-sensitive species. A pronounced elevation in the abundance of disturbance-tolerant wildlife can drive numerous cascading impacts on food webs, biodiversity, vegetation structure and people in coupled human–natural systems. There is also concern for increased risk of zoonotic disease transfer to humans and domestic animals from wildlife species with high pathogen loads as their abundance and proximity to humans increases. Here we use field data from 58 landscapes to document a supra-regional phenomenon of the hyper-abundance and community dominance of Southeast Asian wild pigs and macaques. These two groups were chosen as prime candidates capable of reaching hyperabundance as they are edge adapted, with gregarious social structure, omnivorous diets, rapid reproduction and high tolerance to human proximity. Compared to intact interior forests, population densities in degraded forests were 148% and 87% higher for wild boar and macaques, respectively. In landscapes with >60% oil palm coverage, wild boar and pig-tailed macaque estimated abundances were 337% and 447% higher than landscapes with <1% oil palm coverage, respectively, suggesting marked demographic benefits accrued by crop raiding on caloric-rich food subsidies. There was extreme community dominance in forest landscapes with >20% oil palm cover where two pig and two macaque species accounted for >80% of independent camera trap detections, leaving <20% for the other 85 mammal species >1 kg considered. Establishing the population trends of pigs and macaques is imperative since they are linked to cascading impacts on the fauna and flora of local forest ecosystems, disease and human health, and economics (i.e., crop losses). The severity of potential negative cascading effects may motivate control efforts to achieve ecosystem integrity, human health and conservation objectives. Our review concludes that the rise of native generalists can be mediated by specific types of degradation, which influences the ecology and conservation of natural areas, creating both positive and detrimental impacts on intact ecosystems and human society.

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Key words: abundance, camera trapping, edge effects, fragmentation, hunting, plant–animal interactions, trophic cascades, wildlife ecology.

CONTENTS

I. INTRODUCTION

(1) Disturbance-tolerant wildlife

There are numerous reasons why native wildlife thrives near humans and human-modified landscapes, including favourable habitat features, foraging opportunities or reduced predation and competition (Gaynor *et al.*, 2019; Filgueiras *et al.*, 2021). Native terrestrial mammals are sustained in a variety of human natural systems, where they are part of food webs, contribute to ecosystem processes and in turn provide humans with ecosystem services (Apfelbeck *et al.*, 2020; Collins, Magle & Gallo, 2021). These positive impacts are balanced by deleterious effects if wildlife poses risks to humans and livestock, such as direct attacks, *via* zoonotic diseases, or damage to crops or other products (Luskin *et al.*, 2017*b*, 2021*b*; Gibb *et al.*, 2020). Human tolerance of wildlife also depends on conservation threat levels. For example, Critically Endangered pangolins (*Manis javanica*) are tolerated in Singapore despite elevated zoonotic disease risks (IUCN, 2019; Nursamsi *et al.*, 2023), while Least Concern civets and bats hosting viral pathogens, including Nipah, SARS and likely COVID-19, may not be tolerated (Yu *et al.*, 2018; Gibb *et al.*, 2020; Dehaudt *et al.*, 2022; Dunn *et al.*, 2022). The densities of human commensal wildlife also shape attitudes towards the species and the magnitude of their positive or negative impacts.

(2) Wildlife in degraded habitats

Over 70% of the world's remaining forests are within 1 km of an edge (Haddad *et al.*, 2015). The increasing proportion of edge habitat negatively affects forest specialists and increases access for hunters, who preferentially target large-bodied vertebrates (Peres, 2001; Benítez-López *et al.*, 2017). While many species respond negatively to forest edges, a subset of generalist species can thrive in these degraded areas, particularly those species that can exploit disturbed and human-modified habitats and resources (Gibson, 2011; Luskin *et al.*, 2017*b*). These 'winners' can even reach hyperabundance, greatly exceeding natural densities supported by undisturbed habitats and consequently produce negative impacts on other native fauna and flora (Filgueiras *et al.*, 2021).

II. WILDLIFE HYPERABUNDANCE

(1) Definition

We define hyperabundance in native mammals as at least a doubling of their long-term population density, compared with similar habitats, that is driven by non-natural, human-caused conditions. This definition takes into account the known variation in densities within species that span multiple ecosystems (e.g. grasslands *versus* deciduous forests) or when they are closely tied to predator–prey dynamics (Berryman, 1992). Species like rodents with *r*-selected life histories (prolific reproduction, high mortality, short-lived) may appear predisposed to hyperabundance since they can double their populations within a single year (Fryxell, Sinclair & Caughley, 2014), but we reserve the term hyperabundance for situations with persistently elevated densities across multiple years (e.g. Gibson *et al.*, 2013; Moore *et al.*, 2022).

(2) Drivers of hyperabundance

Wildlife hyperabundance in degraded landscapes can arise through several processes. Species traits associated with hyperabundance may include being habitat and dietary generalists that naturally thrive in ecotones and edges, or species with high fecundity whose populations can respond to changing resources or withstand hunting pressure (Terborgh & Estes, 2013; Filgueiras *et al.*, 2021). Hyperabundance is also found in species that leave natural areas to exploit anthropogenic food subsidies (i.e. crop raiding) and in species considered unpalatable due to food taboos or that are uninteresting for the pet and medicine trade (Oro *et al.*, 2013; Luskin *et al.*, 2014, 2017*b*).

(3) Hyperabundance globally

Examples of hyperabundance can be found in a variety of species and ecosystems, indicating this is a global phenomenon (Fig. 1). Hyperabundant native generalists are often associated with humans and cause severe ecological damage (Estes *et al.*, 2011; Luskin *et al.*, 2017*b*) and alter plant and animal diversity (Estes *et al.*, 2011; Terborgh & Estes, 2013; Dirzo *et al.*, 2014; Ivey *et al.*, 2019). Hyperabundant species may also be associated with human–wildlife conflict such as crop raiding (Luskin *et al.*, 2014; Taylor *et al.*, 2016), property damage (Barrios-Garcia & Ballari, 2012), and outbreaks of zoonotic diseases such as rabies and Lyme disease (Levi *et al.*, 2012; Gibb *et al.*, 2020). There is an especially urgent need for a large-scale synthesis to understand the patterns, drivers, and consequences of hyperabundant generalist species in regions suffering high rates of biodiversity loss, habitat degradation, and histories of zoonotic disease emergence, all of which may be aggravated by high human population densities.

(4) Hyperabundance in Southeast Asia

Hyperabundance in Southeast Asia is poorly understood (Amir *et al.*, 2022*a*). To date, clear results have only been reported for Malayan field rats (*Rattus tiomanicus*) on man-made islands (Moore *et al.*, 2022), wild boar (*Sus scrofa*) in one forest in Peninsular Malaysia (Ickes, 2001; Luskin *et al.*, 2017*b*), and sporadic reports suggesting high densities of long-tailed macaques (*Macaca fascicularis*) that require management in Peninsular Malaysia (Choong *et al.*, 2021). There are no clear regional trends for pigs and macaques and these taxa are actually presumed to be declining in most accounts (Luskin & Ke, 2017; Luskin *et al.*, 2018, 2021*b*, 2023; Keuling & Leus, 2019; Ke & Luskin, 2019; Ruppert *et al.*, 2022; Hansen *et al.*, 2023). In Southeast Asia, there are reports of wild boars and bearded pigs *Sus barbatus* benefiting from oil palm but these all arose from single-landscape studies. Studies at Pasoh Forest Reserve in Peninsular Malaysia (Ickes, Dewalt & Appanah, 2001; Luskin *et al.*, 2017*b*), Sumatra (Luskin *et al.*, 2014), and Sabah, Borneo (Love *et al.*, 2017) have shown positive responses of wild boars and bearded pigs to oil palm. There is equally as much work suggesting wild boars and bearded pigs are declining in the region (Harrison *et al.*, 2016; Luskin *et al.*, 2018) with the lethal onslaught of African Swine Fever threatening extirpations and extinctions (Luskin *et al.*, 2021*b*, 2023). For macaques, recent work suggested that pig-tailed macaques *Macaca nemestrina* are increasingly threatened, leading to the IUCN *Red List* upgrading their threat status from Vulnerable to Endangered, i.e. the opposite of hyperabundance (Ruppert *et al.*, 2022).

(5) Study species

We chose to focus on four pig and macaque species that have importance ecologically, culturally, and/or economically. These species are also the most frequently detected in camera trapping studies in Southeast Asia, together often accounting for >50% of detections: wild boar (*Sus scrofa*), bearded pig (*Sus barbatus*), pig-tailed macaque (*Macaca nemestrina*) and long-tailed macaque (*Macaca fascicularis*). These species possess several characteristics that make them prime candidates for negatively related to all types of degraded habitats since they are not considered edge specialists but are found in fragmented and logged forests and are actively hunted in their core range in Borneo; and (*iv*) oil palm might be driving pig and macaque densities in nearby forests, as crop-raiding pigs have been argued to benefit from oil palm kernel food subsidies in three previous studies at the individual-landscape level and macaques are edge-specialist frugivores. For all relationships, we predict that macaques will show stronger associations to habitat measured at local scales (~1 km^2) and pigs at larger scales (20 km^2) because pigs are more vagrant and exhibit less site fidelity (Melletti & Meijaard, 2017). We also verify if habitat associations gleaned from camera trap detections are also present in independent studies estimating densities.

III. METHODS

(1) Approach

We used a multi-scale approach because these adaptable species may respond differentially to local and landscape-level factors and adjust their movements and home range sizes (Thornton, Branch & Sunquist, 2011; Hansen *et al.*, 2020). First, we collated published density estimates to determine the drivers and absolute magnitude of changes in pig and macaque densities. Second, we utilised published camera trapping records to examine whether pigs and macaques show community dominance in degraded forests and near oil palm plantations at the landscape scale (comparing landscapes). Finally, we utilised new camera trapping records to test whether pigs and macaques became hyperabundant in degraded forests near plantations at the local scale (within landscapes).

(2) Study area

Our study area was defined as mainland Southeast Asia, Sumatra and Borneo for all landscape-level and camera-level analysis (Fig. 2A), excluding Java, the Philippines and anything east of Wallace's line. This study area was selected to match areas that share relatively consistent natural habitat conditions with predominately evergreen tropical forests and include the native distributions of at least three of our four study species (see online supporting information, Fig. S1).

For our landscape-level analyses of published densities and relative abundances in camera trapping, the exact sampling locations were obtained from the methods sections of published studies, or, when unavailable, we extracted coordinates from the study map (see Table S1 for density estimates and Tables S2 and S3 for relative abundance). If positional accuracy was a concern, we contacted the original authors for these details. Most camera trapping deployments covered large areas (10–1000 km^2) and were not arranged in a perfect grid or circle. To account for the lack of precision in identifying the exact sampling area centroids, we generated covariates describing the landscapes within a 20 km radius (1256 km^2) using Geographic Information System (GIS) zonal statistics in the spatial analysis software QGIS (see Table S4 for sources of covariates used in generating species abundance estimates; Fig. S2). For the local-scale analyses from camera-level capture histories, we extracted covariates describing the areas within a 1 km radius (~3.14 km^2) of each camera. This distance was chosen as intermediate between the average home range size estimates for wild boars and macaques and has been used for studies focused on either genus (José-Domínguez, Savini & Asensio, 2015; Rayan & Linkie, 2020).

(3) Extracting standardised covariates to describe study areas

We focused on two covariates in testing the underlying drivers of pig and macaque hyperabundance and/or community dominance (Table S4). We used the Forest Landscape Integrity Index (FLII) values with 300 m pixel resolution to assess the influence of habitat degradation (edges, fragmentation, and logging; Grantham *et al.*, 2021). The FLII (hereafter 'forest integrity') is a globally consistent landscape-level index that incorporates forest loss, logging, and edges, as well as inferred effects from fragmentation and the loss of connectivity and is scaled between values of 0 = most degraded to 10 = most intact. Next, we quantified the percentage cover of oil palm in our study landscapes using the CRISP 2015 land cover map of Southeast Asia (Miettinen, Shi & Liew, 2016). This GIS layer includes 18 landscape types (including oil palm) at 250-m resolution.

There are various benefits and errors when integrating spatial covariates from many studies into standardised and consistent GIS layers. In particular, there may be some inaccuracies when extracting covariates from older studies (pre-2010) using GIS layers created after 2015, especially for the dynamic landscapes of Southeast Asia. However, the GIS layers we used rely upon numerous remote-sensing images obtained over multiple years and are the most robust sources currently available. For example, a pre-2010 study in an intact forest landscape may have suffered extensive clearing and oil palm establishment since 2010, and thus our method may incorrectly describe these coordinates as degraded with oil palm, when in fact at the time it was intact forest. Given recent ongoing clearing outpacing any reforestation in the study region, the direction of this bias is almost always to overestimate disturbance-sensitive species' presence in degraded areas, which reduces our statistical power. As a result, we likely underestimate true effect sizes, thereby yielding results that should be considered conservative.

(4) Macaques and wild boar density estimates

We collated published densities of pigs and macaques using a *Web of Knowledge* search performed with the search terms including common and scientific names AND dens* AND

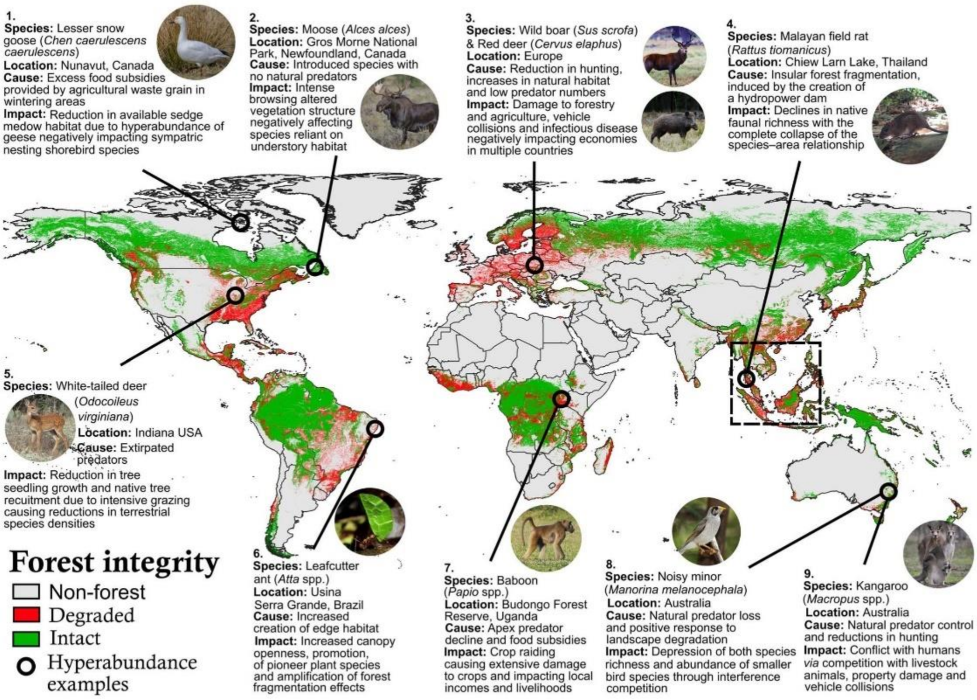

Fig. 1. Examples of hyperabundant native wildlife. The dashed square indicates our study area. Colours on the map represent the Forest Landscape Integrity Index (FLII), which incorporates forest size, distance to edge, degree of fragmentation, and logging, with a range of 0 (most disturbed) to 10 (most undisturbed). Degraded forest was defined as cells with FLII scores from 0 to <7 (red) and intact forest as scores from 7 to 10 (green) using data generated by Grantham *et al.* (2021). Oil palm is shown in purple. References for examples of hyperabundance: 1, Flemming *et al.* (2019); 2, Rae *et al.* (2014); 3, Valente *et al.* (2020); 4, Moore *et al.* (2022); 5, Shelton *et al.* (2014); 6, Meyer *et al.* (2009); 7, Taylor *et al.* (2016); 8, Melton *et al.* (2021); 9, Wilson & Edwards (2019).

reaching hyperabundance: they have generalist omnivorous diets, are found in disturbed forests, and exhibit rapid reproductive rates (Love *et al.*, 2017; Luskin & Ke, 2017; Ruppert *et al.*, 2018, 2022; Ke & Luskin, 2019; Hansen *et al.*, 2020; Luskin *et al.*, 2023). These traits could potentially allow their populations to respond rapidly to changes in food, predation, and competition, and all four species are gregarious and group living and thus may be able to achieve higher densities than territorial solitary animals.

Establishing the population trends of pigs and macaques is imperative since they are linked to cascading impacts on the fauna and flora of local forest ecosystems, and human health and economics (Bueno *et al.*, 2011; Gibson *et al.*, 2014; Luskin *et al.*, 2014, 2017*b*; Cuevas *et al.*, 2020). Pigs (*Sus* spp.) and macaques (*Macaca* spp.) host high pathogen loads and are known to carry several diseases, including brucellosis, leptospirosis, Nipah, tuberculosis and Japanese encephalitis (discussed further in Section V.5). These species also share high rates of immune similarity with humans, with recent evidence of simian malaria outbreaks in Central Kalimantan, Indonesia (Lee *et al.*, 2011; Barrios-Garcia & Ballari, 2012; Setiadi *et al.*, 2016) acting as disease reservoirs and providing considerable potential for zoonotic disease transfer to humans (Plowright *et al.*, 2017; Shah *et al.*, 2018; Gibb *et al.*, 2020).

(6) Research questions and hypotheses

Here we investigate if abundance is related to environmental variables (e.g. elevation) or disturbance variables (e.g. edges, logging, oil palm). We hypothesise that (*i*) macaque abundance will be positively related to all types of habitat degradation since they are edge specialists and rarely hunted; (*ii*) wild boar abundance will be unrelated to degraded habitats since they are edge specialists and are hunted to variable extents throughout the region; (*iii*) bearded pigs will be

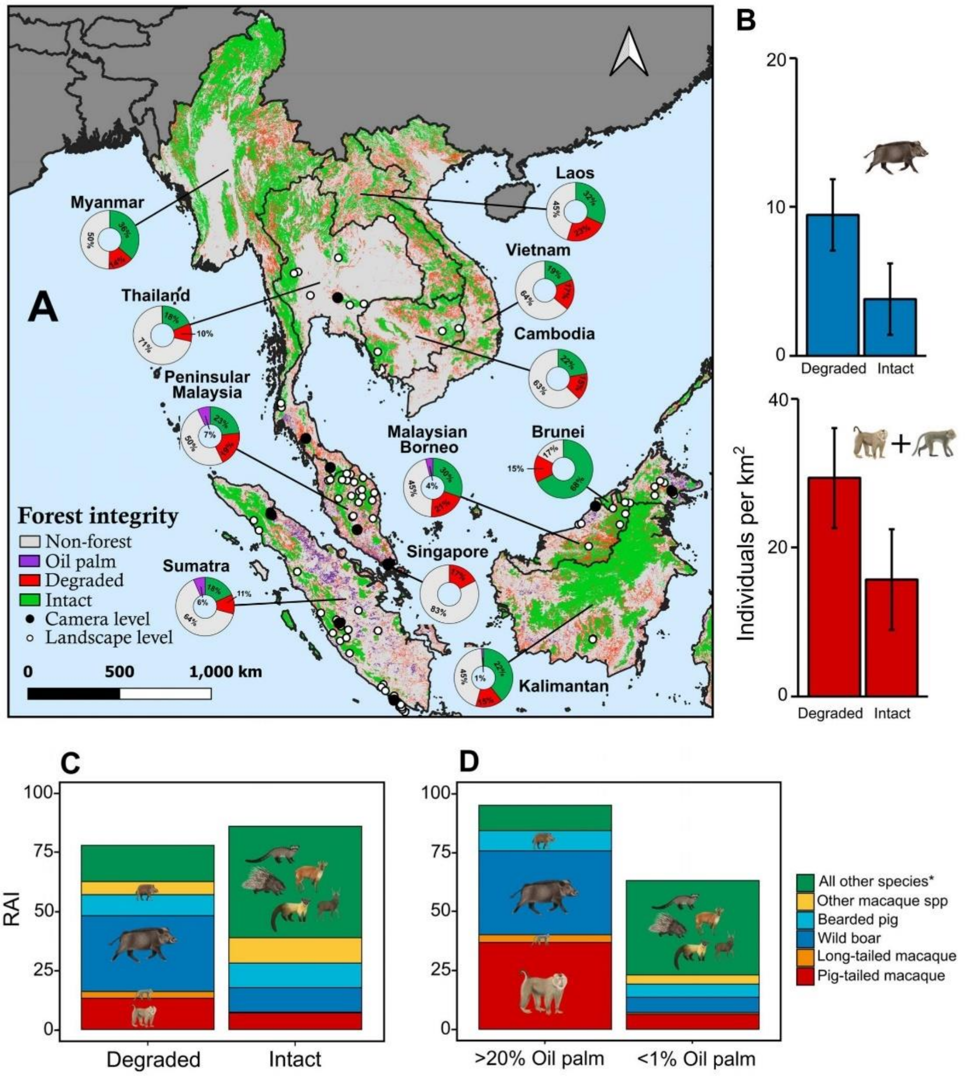

Fig. 2. Study region and study sites within Southeast Asia (A), pig and macaque densities (B) and relative abundance index (RAI; independent photographs per 100 trap nights) in camera trapping studies (C, D). We compared RAI between degraded [Forest Landscape Integrity Index (FLII) 0 to <7) and intact landscapes (FLII 7–10) (C) and between areas with high (>20%) and low (<1%) oil palm cover (D). In (A), the doughnut charts depict the percentage of each landscape classification per country. (B) provides the mean ± S.E.M for 44 and 19 published density estimates of wild boar (top) and long-tailed and pig-tailed macaques (bottom), respectively, across the study region. In (C) and (D), stacked bar charts show the average estimated RAI per species from 117 published camera trapping studies. *All other species includes 80 terrestrial vertebrates >1 kg. Statistical tests and box plots for (B–D) are presented in Figs S4–S6.

Asia. We also investigated citations within the identified papers for density estimates and included any suitable papers. This resulted in 23 density estimates for macaques (nine for pig-tailed macaques and 14 for long-tailed macaques), across 13 landscapes from 14 publications. We found a total of 79 density estimates for wild boar across 41 landscapes from 47 publications; there were no bearded pig density estimates so they were excluded from this analysis (Table S1). We estimated mean densities in intact and degraded forests using linear mixed-effects models (LMMs) with the R-package *lme4* (Bates *et al*., 2015), with landscape included as a random effect to account for multiple observations from the same area. As there are relatively few density observations for macaques, we grouped pig-tailed and long-tailed macaques (same genus and with similar diets/behaviour) and included both species and landscape as random effects (Table S5). We feel it is appropriate to pool these two species in this analysis. We note that the original density estimates did not all employ standardised sampling or analytical methods and this could introduce additional noise.

(5) Pig and macaque abundance among landscapes

We examined the landscape-level predictors of pig and macaque abundance using capture rates from published camera trapping studies in Southeast Asia (Fig. 2C, D). We identified published camera trapping studies using a *Web of Knowledge* search performed with the criteria 'camera trap' AND any of our study countries, as well as Asia*, Malay*, Thai*, Sumatr* and Born*. We also performed the same search in *Google* to locate grey literature and academic theses. We retained studies that used unbaited camera deployments in forest, and which reported the full species capture lists (number of independent photographs of all mammals >1 kg) and the trapping effort (trap nights) (Tables S2 and S3). We refer to the area sampled as a 'landscape', which was usually a national park, production forest, or collection of nearby forest patches, and our final sample size was 164,055 detections of 89 species from 43 studies and 58 landscapes. We used 20-km radius buffers to extract landscape covariates providing average forest integrity values and landscape-scale percentage oil palm cover. We used published camera trap data to assess relationships between pig and macaque capture rates and landscape covariates (forest integrity and % oil palm cover). We used generalised linear mixed models (GLMMs) with the number of independent captures as the response variable (count data, assuming Poisson distribution), controlling for sampling effort as a model offset, and including 'landscape' as a random effect. Significance was assessed using the *z*-value and Satterthwaite approximations for degrees of freedom using *lmerTest* in R (Kuznetsova, Brockhoff & Christensen, 2017). Since we make comparisons within species and using similar sampling protocols, we assume that detectability does not vary systematically with our covariates, and therefore infer that differences in capture rates reflect true differences in abundance. We also used relative abundance index (RAI) from the published camera trap data to run LMMs to assess community dominance of pigs and macaques. Our RAI comparisons were performed by separating forest integrity into two groups [high (values 7–10) and low forest integrity (0 to <7)] and separating oil palm landscapes into high (area > 20%) and low oil palm cover (area <1%), and we ran separate LMMs for all four pig and macaque species.

(6) Local pig and macaque abundance within landscapes

We conducted 20 new camera trapping sessions in 10 landscapes in Thailand (two sites), Peninsular Malaysia (two sites), Singapore (one site), Sumatra (three sites) and Borneo (two sites) to assess the effects of local habitat characteristics on relative abundances (see Table S6 and Appendix S1 for site description and trap deployment details). We produced detection history matrices using the total number of individuals detected within a sampling occasion of 3 days to reduce zero-inflation, and spatially resampled all cameras into hexagonal grid cells of equal size (0.86 km^2, hereafter 'sampling units') to satisfy spatial independence (Fig. S3; see Appendix S1 for detailed methods; Rayan & Linkie, 2016). Habitat covariates were averaged when there were multiple cameras within the same cell. We used hierarchical N-mixture (NM) models to estimate the relative abundance of pigs and macaques while accounting for imperfect detection using the *pcount()* function in *unmarked* in R (Royle, 2004; Fiske & Chandler, 2011). NM models provide an unbiased relative abundance metric (hereafter 'estimated abundance'), allowing for robust comparisons across multiple surveys for species that cannot be identified individually (Royle, 2004). We included 'landscape' as a fixed effect to account for three landscapes sampled over multiple trapping sessions and included sampling effort as a fixed effect on the detection probability formula to account for multiple cameras in the same grid cell (Table S7). We ran the same NM models for all species and tested if estimated abundance varied with forest integrity and percentage of oil palm plantations within 1 km of each camera.

IV. RESULTS ON HYPERABUNDANCE IN SOUTHEAST ASIA

(1) Densities

Population densities of wild boar were 148% higher (LMM: $t_{50.1} = -2.35$, $P = 0.023$) in degraded landscapes (mean ± S.E.M = 9.5 ± 1.9 individuals/km^2) compared with intact landscapes (3.8 ± 2.4 individuals/km^2) (Fig. 2B; see Fig. S4 for results of statistical tests). Macaques (both species combined) were 87% higher (LMM: $t_{15.2} = -2.03$, $P < 0.059$) in degraded landscapes (29.4 ± 5.9 individuals/km^2) compared with intact landscapes (15.7 ± 6.7 individuals/km^2) (Fig. 2B). Pig-tailed macaques, when considered separately, showed densities 69.7% higher in degraded landscapes (24.1 ± 6.7) compared with intact landscapes (14.2 ± 0.7) (LMM: $t_2 = -13.33$, $P < 0.005$; Table S5). Long-tailed macaques could not be modelled separately due to insufficient data from intact forest sites for a statistical test but the mean density for degraded landscapes was 520% higher with 31 individuals/km^2 compared to 5 individuals/km^2 for intact forest.

(2) Community dominance

When comparing communities from intact *versus* degraded forest landscapes, the community dominance of pigs and macaques (i.e. the total RAI of the four focal species) rose from 32.7% to 73.2% of all independent captures, and when comparing low (<1%) to high (>20%) oil palm cover, the community dominance of pigs and macaques rose from 30.4% to 88.7% (Fig. 2C,D; see Tables S8 and S9 and Figs S5 and S6 for data from individual species). These shifts in community dominance were driven both by higher detection rates of the four generalist species and lower detection rates of forest specialists (Fig. 2C, D). In fact, pooled detections of the other 85 wildlife species >1 kg were 63.9% lower in degraded landscapes (LMM: $t_{65} = 2.95$, $P < 0.004$; Fig. 2C) and 75.5% lower in high (>20%) oil palm cover landscapes (LMM: $t_{56} = 2.88$, $P < 0.005$; Fig. 2D).

(3) Landscape-level determinants of hyperabundance

When examining habitat relationships using Poisson GLMMs with detections as a response variable and the continuous landscape-level predictors we found strong but not entirely consistent patterns. Long-tailed macaques showed a negative relationship with forest integrity (GLMM: $z = 5.81$, $P = 0.002$), while bearded pigs showed a significant positive relationship with forest integrity (GLMM: $z = 3.94$, $P = 0.008$). There were no significant relationships between forest degradation and wild boar or pig-tailed macaques (Fig. 3C). Relationships between the percentage oil palm in the landscape and wild boar and long-tailed macaque abundance were significantly positive (GLMM: $P < 0.01$ for both species) while no significant relationship was found for pig-tailed macaques or bearded pigs (Fig. 3D).

(4) Local determinants of hyperabundance

At the local scale, the estimated abundance from NM models was higher for three of the four species when sites with the minimum and maximum observed forest degradation were compared: wild boar = +196% 95% confidence interval (CI) = 195.6–197.3%), long-tailed macaque = +456.7% (95% CI = 437.4–476.7%) and pig-tailed macaque = 62.9% (95% CI = 62–63.9%; all NM: $z = <-5$, $P < 0.0001$) (Fig. 3A). However, abundance was 77.8% (95% CI = 76.3–79.3%) lower for bearded pigs at the most degraded sites ($z = 8.5$, $P < 0.0001$; Table S7). Estimated abundance was higher for all four species when comparing between landscapes with the minimum (<1%) and maximum (>60%) observed oil palm cover [wild boar = +336.7% (95% CI = 306.5–369.3), bearded pig = +655.3% (95% CI = 571.1–750.1), long-tailed macaque = +9036.8% (95% CI = 8899.8–9175.9%), pig-tailed macaque = +447.3% (95% CI = 426.6–468.7; all NM: $z = >15$, $P < 0.0001$; Fig. 3B; Table S7].

V. THE CAUSES AND CONSEQUENCES OF HYPERABUNDANCE

(1) Pig and macaque hyperabundance

We document the hyperabundance of pigs and macaques across Southeast Asia. The *Sus* and *Macaca* genera now comprise the majority of all terrestrial vertebrates detected on camera traps in disturbed forests, constituting 73.2% and 88.7% of all captures in degraded forests and landscapes with >20% oil palm cover, respectively. These results show strong community dominance. Examples of hyperabundant native generalists can be found globally, including baboons in Africa, mesopredator release in North America and deer and pig species in Europe. Hyperabundance is often triggered by a reduction in top-down control by native predators, or by the presence of food subsidies, especially for disturbance-tolerant species and high-fecundity species (Rae, Whitaker & Warkentin, 2014; Luskin *et al.*, 2017*b*; Flemming *et al.*, 2019; Valente *et al.*, 2020).

Based on our definition of hyperabundance in mammals, describing the elevated numbers of Southeast Asia's pigs and macaques as hyperabundance is warranted for several reasons. First, our comparisons are limited to habitats that are predominantly tropical evergreen forests and include many observations from the same landscapes. Second, our study includes observations extending over more than 20 years, suggesting the observed trends are not ephemeral. Third, neither pigs nor macaques fit cleanly into either *r*- or *K*-selected life histories. Compared to similarly sized species, pigs are able to reproduce rapidly producing up to two large litters per year under ideal conditions with plentiful resources (Bywater *et al.*, 2010; Croft *et al.*, 2020) while also being comparatively long-lived (Fryxell *et al.*, 2014). Fourth, we identify *in situ* anthropogenic environmental drivers including habitat degradation and food subsidies from oil palm plantations as deviations from natural long-term conditions.

(2) Degraded forest and agricultural food subsidies

At the landscape scale, habitat associations with forest degradation were unclear for wild boar and pig-tailed macaques, whereas long-tailed macaques performed better in degraded landscapes and bearded pigs performed worse. High oil palm coverage (>20%) elevated the abundance of both wild boar and long-tailed macaques. Densities at the landscape scale were also higher in degraded habitats for both wild boar and macaques. At the local scale, which considered the 3.14 km^2 areas around cameras, habitat degradation and

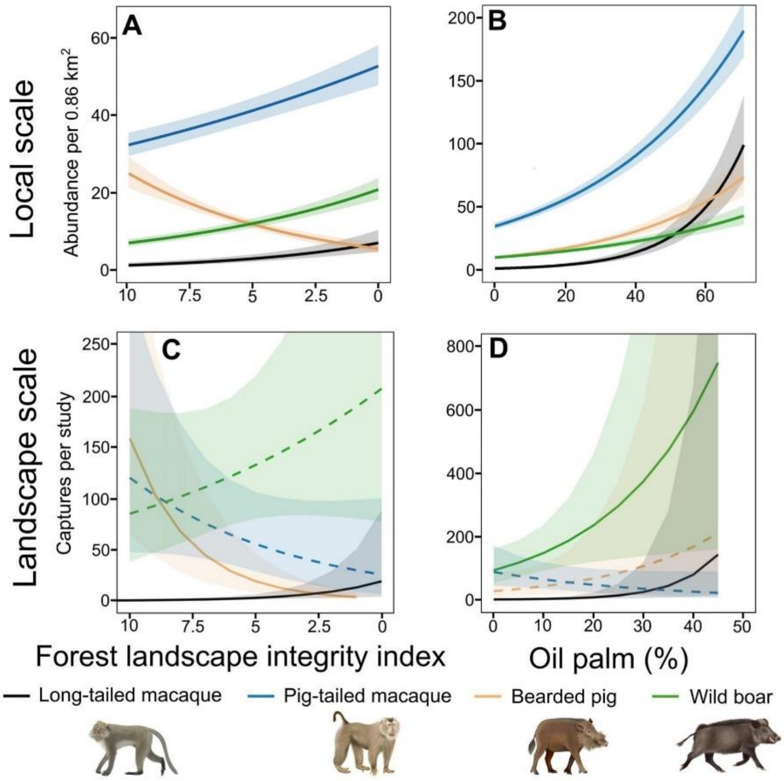

Fig. 3. Pig and macaque abundance in relation to forest integrity and oil palm agriculture in the landscape. The local-scale panels (A, B) show estimated abundance per 0.86 km^2 hexagonal grid cell across 10 newly sampled landscapes in Southeast Asia from N-mixture detection-corrected hierarchical modelling with covariates measured within 1 km of each camera. The landscape-scale panels (C, D) show estimated detections per study from generalised linear mixed models (GLMMs) with covariates averaged over 20 km radius study areas ($N = 117$ published data sets). Solid lines indicate a significant trend ($P < 0.05$), and shaded regions show 95% confidence intervals. Note forest integrity is descending so that intact landscapes are on the left and more degraded landscapes are on the right.

oil palm cover were consistently associated with elevated population abundance of wild boar and macaques. The positive association between bearded pigs and forest integrity, both within and across landscapes, may suggest a preference for primary forest adjacent to oil palm plantations. This is supported by a previous study in Borneo showing that bearded pigs utilise oil palm landscapes but prefer adjacent forested areas for a wider range of their behaviours (Love *et al.*, 2017). Taken together, our results likely reflect both that degraded areas have higher densities of pigs and macaques, and that mobile individuals (and groups) within these landscapes prefer edges near oil palm, as opposed to forested areas further from edges.

Our results documenting the highest pig and macaque densities near oil palm plantations align with other work in Malaysia showing abnormally high wildlife abundances within forest fruit gardens (Moore *et al.*, 2016). This suggests that supplementary food can release wildlife from natural bottom-up regulation imposed by resource scarcity, which may be especially important in Southeast Asian forests where the fruiting phenology of most canopy trees shows a supra-annual masting cycle (Curran & Leighton, 2000). Only certain habitat-generalist species can access food subsidies beyond forest edges, such as those provided by oil palm plantations, so there may be asymmetric competition with other herbivores. Habitat and dietary generalists such as pigs and macaques that thrive in ecotones frequently raid cultivated crops, and consume both native plant material and human refuse from farmers living within oil palm landscapes (Bieber & Ruf, 2005; Barrios-Garcia & Ballari, 2012), likely out-competing deer, tapirs, and other vertebrate herbivores and omnivores in these degraded habitats.

(3) Other factors supporting hyperabundance

There are three other reasons for the success of pigs and macaques in degraded forest landscapes. First, both pigs and macaques have high fecundity, allowing them to exploit resources rapidly, tolerate hunting pressure, and recover quickly from disturbances. Second, large mammalian predators often avoid degraded habitats and oil palm, indirectly benefitting prey species capable of exploiting those same areas (Brodie, Giordano & Ambu, 2015; Luskin, Albert & Tobler, 2017*a*). Third, pigs and macaques are rarely targeted by hunters throughout regions where Islamic religious practices are observed, since the Halal diet forbids pork and fanged animals, including macaques (Luskin *et al.*, 2014). The exception is areas in Borneo occupied by the Dayak people who often hunt bearded pigs (Luskin *et al.*, 2014; Kurz *et al.*, 2021, 2023).

(4) Consequences of wildlife hyperabundance for forests

Our findings have important conservation implications. Hyperabundant omnivorous ungulates and primates can alter vertebrate food webs through direct predation of smaller animals such as rodents, reptiles and birds (Ruppert, Mansor & Shahrul Anuar, 2014; Ruppert *et al.*, 2018; Law, Ruppert & Holzner, 2018), disturb nesting sites (Mori *et al.*, 2021), exert exploitative competition of a shared resource (Ilse & Hellgren, 1995; Barrios-Garcia & Ballari, 2012) and induce indirect effects through degradation of understory structure (Luskin *et al.*, 2019, 2021*a*; Mori *et al.*, 2021). Altered understory structure occurs through intense soil disturbance and direct seed/seedling predation (Bueno *et al.*, 2011; Cuevas *et al.*, 2020) and promotes the spread of invasive plant species (Fujinuma & Harrison, 2012), facilitates liana proliferation on host trees (Luskin *et al.*, 2019), and alters tree diversity (Luskin *et al.*, 2017*b*, 2021*a*). Further, pig soil disturbances in their invasive range are thought to impact carbon storage potential by driving greenhouse gas emissions representing up to 0.4% of annual land-use and forestry emissions (Terborgh & Estes, 2013; Dirzo *et al.*, 2014; Chanthorn *et al.*, 2019; O'Bryan *et al.*, 2021), and there is little reason to suggest that their hyperabundance within native ranges would not produce similar levels of emissions. The sustained hyperabundance of pig and macaque populations in degraded forests and near oil palm plantations may deplete natural forest tree seeds during a mast, thus reducing seedling recruitment and future forest regeneration, and thereby undermining the strategy of predator satiation (Janzen, 1974; Curran & Leighton, 2000; Jia *et al.*, 2018; Luskin *et al.*, 2019, 2021*a*; Williams *et al.*, 2021). The influence of hyperabundant macaques on biotic communities is less well understood, but we note that their seed-dispersal capacity appears to be limited for large-seeded plant species (Nakashima & Sukor, 2010).

(5) Consequences of wildlife hyperabundance for humans

The hyperabundance of pigs and macaques also has important impacts on humans, since they drive economic damage from crop-raiding and display highly aggressive behaviour towards humans, even in urban settings (Priston & McLennan, 2013; Luskin *et al.*, 2017*b*; Ilham *et al.*, 2017; Balasubramaniam *et al.*, 2020). Pigs are an amplifying host in which zoonotic viruses can modify for transmission to humans, whereas macaques can act as both reservoirs and amplifiers. The rise of pigs and macaques has been implicated in a higher potential for zoonotic disease transmission (Gibb *et al.*, 2020). For instance, zoonotic diseases such as malaria *Plasmodium knowlesi* have a geographic range limited by their mosquito vectors and simian hosts (Moyes *et al.*, 2014), but as landscapes become increasingly degraded zoonotic host populations both expand and also increase their proximity to humans, elevating disease risk. This is evident in Malaysian Borneo where human malaria outbreaks – mediated by macaques as zoonotic carriers (Fornace *et al.*, 2016) – have increased. Cases of the zoonotic disease monkeypox have increased throughout 2022; this virus was first named and classified from samples taken from long-tailed macaques in Denmark in 1958 (Magnus *et al.*, 2009; Liu *et al.*, 2022). Nipah is spread by wild boars in Malaysia and Singapore (Yu *et al.*, 2018), and tick-borne disease transfer from wild boars occurs in Europe (Hrazdilová *et al.*, 2021; Castillo-Contreras *et al.*, 2022). Both species also carry a variety of helminths (e.g. parasitic worms) that plague human health in developing countries. Domestic livestock are also threatened by disease transfer from pigs, including African swine fever and foot-and-mouth disease (Denstedt *et al.*, 2021).

(6) Managing hyperabundant wildlife

Hyperabundant species can impact humans and local fauna and flora in a multitude of negative ways, requiring extensive control measures (Taylor *et al.*, 2016; Wilson & Edwards, 2019; Moore *et al.*, 2022). There are significant efforts to manage hyperabundant pig and macaque populations in Malaysia, Singapore and Indonesia (Luskin *et al.*, 2014; Lamperty *et al.*, 2023). Population control through cage trapping, culling, hunting and sterilisation may be effective when adequate resources are available (Priston & McLennan, 2013; Luskin *et al.*, 2014; Croft *et al.*, 2020). However, the high fecundity of these species makes control difficult as success (e.g. >50% population decline) would require high-intensity management for prolonged if not indefinite periods (Annapragada *et al.*, 2021).

Management efforts to limit pig and macaque access to oil palm have largely failed. Luskin *et al.* (2017b) describe an attempt by the FELDA oil palm company to prevent wild boar from killing oil palm seedlings in Peninsular Malaysia. They constructed a 1 m trench with 1.5 m solid metal sheeting mounted vertically above the trench and stretching along approximately 5 km of the forest-plantation edge. Within weeks the trench had flooded, the pigs enjoyed these areas as pseudo-wallows, and then they dug underneath or pushed over the compromised fence. Macaque species can similarly negotiate fencing with ease (Mysterud & Rolandsen, 2019). Likewise, as semi-natural buffer zones between forests and plantations are also likely to be advantageous for pigs and macaques, such 'designer landscapes' are unlikely to improve the situation (Reidy, Campbell & Hewitt, 2008; Koh, Levang & Ghazoul, 2009). Another focus should be on limiting further oil palm expansion into surrounding intact forests, and instead exploiting already disturbed areas (Luskin & Potts, 2011). Long-term monitoring data focused on species abundance are essential to assessment of baseline population levels and of the effectiveness of ongoing management techniques. In the meantime, we recommend the prevention of future development of agriculture within close proximity to intact forests which could provide food subsidies to generalist species.

VI. KNOWLEDGE GAPS AND CAVEATS

(1) The roles of predators, competitors, and hunting

The role of hyperabundant native generalists in providing supplementary prey for carnivores has received little attention, nor has the role of hyperabundant native generalists on competitors, except for rodents on island fragments in Thailand (Moore *et al.*, 2022). Likewise, there is little known regarding the role of hunting in controlling pig and macaque populations, although this has been attempted for macaques in Peninsular Malaysia, and Dayak hunters in Sarawak nearly extirpated bearded pigs from a small forest adjacent to oil palm (Harrison *et al.*, 2016). Especially poignant in the region is the role of religion and culture in shaping hunting, wildlife abundance, and cascading impacts on forest ecology (Kurz *et al.*, 2021, 2023). Further research should also focus on the potential cascading impacts imposed by hyperabundant pigs and macaques in Southeast Asia, including their effects on vegetation structure, faunal communities, and human–wildlife conflicts. There is also an urgent need to improve disease monitoring of these species in this region, especially at edges where they are most likely to interact with domestic animals and humans. Further work on the top-down control of pigs and macaques is required to understand fully the mechanisms driving hyperabundance of generalist species in tropical forest regions (Amir, Sovie & Luskin, 2022b; Hendry *et al.*, 2023).

(2) Caveats

Some trade-offs were required in collating this data set for larger Asian vertebrates to make regional inferences. Data sources vary in quality and in the methodology used to generate the values we included in our synthesis. We sought to overcome this by triangulating results using different forms of analysis to increase confidence in the trends reported. We advise that conditions may change rapidly due to disease (e.g. African swine fever), changes in harvesting (macaque capture for medical testing) or lethal management. For example, both *S. scrofa* and *S. barbatus* populations have crashed recently due to African swine fever outbreaks across the region (Luskin *et al.*, 2023). The rapid spread of this disease could have been aided by the high population densities reported here.

VII. CONCLUSIONS

(1) The wildlife origins of the COVID19 pandemic and alarming recent work (Gibb *et al.*, 2022) show that generalist mammals persisting in human-modified ecosystems often host high pathogen loads and pose serious zoonotic disease risks, emphasising the importance of new research in these areas.

(2) We reviewed the evidence for two key generalist groups in Southeast Asia, a biodiversity and zoonotic disease risk hotspot. Specifically, we examined population trends for pigs and macaques, which are known zoonotic disease reservoirs. We show that these species are more common in most degraded areas, but the most pronounced increases – to a level we consider hyperabundant – were contingent on the nearby presence of oil palm agriculture in the landscape. This supports a dominant role of food subsidies in non-forested areas shaping wildlife outcomes inside forests, as opposed to increased foraging or habitat quality of degraded forest themselves. These results are likely generalizable to coupled human–natural environments abound across the globe (Goheen, 2016).

(3) These results can inform conservation and epidemiological work in Southeast Asia, and our approach of synthesizing camera trap data can be replicated for other species and regions.

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X. SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Fig. S1. Forest distribution across Southeast Asia and showing percentage of forest within 2 km of an edge per country (A), the Forest Landscape Integrity Index (FLII) used in our analyses (B), the IUCN distribution maps within Southeast Asia, of wild boars (C), pig-tailed macaques (D), bearded pigs (E), and long-tailed macaques (F).

Table S1. Literature review of density estimates for long-tailed macaque, pig-tailed macaque and wild boar with corresponding Forest Landscape Integrity Index (FLII) value.

Table S2. Capture rates of long-tailed macaque, pig-tailed macaque, wild boar and bearded pig with corresponding data sources and oil palm landscape values.

Table S3. Capture rates of long-tailed macaque, pig-tailed macaque, wild boar and bearded pig with corresponding data sources and Forest Landscape Integrity Index (FLII) values.

Table S4. Covariates used for generating species abundance estimates.

Fig. S2. Study sites (A), schematic showing how habitat covariates were extracted in given radius around each camera or study centroid (B), description of the two types of scales of camera trap data reviewed (C), and the two analytical modelling approaches employed (D).

Table S5. Linear mixed model (LMM) output for individual macaque species density estimates for Forest Landscape Integrity Index (FLII).

Table S6. Study site characteristics for new camera trapping.

Appendix S1. Supplementary methods.

Fig. S3. Example from Lambir Hills National Park, Malaysia showing how camera trap locations were resampled into 0.86 km^2 hexagonal grid cells used as the sampling units in the detection history matrix in the N-mixture models.

Table S7. N-mixture modelling of estimated abundance with confidence intervals (CI) and minimum/maximum estimates for long-tailed macaque, pig-tailed macaque, wild boar, and bearded pig.

Fig. S4. Linear mixed-effects model (LMER) outputs for (A) wild boar and (B) macaque densities in response to degraded Forest Landscape Integrity Index (FLII 0 to <7) and intact (FLII 7–10) landscapes.

Table S8. Linear mixed model (LMM) outputs with relative abundance index (RAI) estimates, standard errors and statistical significance in low (<1%) and high oil palm (>20%) landscapes and intact *versus* degraded forest landscapes for long-tailed macaque, pig-tailed macaque, wild boar, bearded pig, other macaque species, and all other species.

Table S9. Total estimated relative abundance index (RAI) and percentage dominance of pigs and macaques (combined) [see Table S8 for linear mixed model (LMM) estimates] in low (<1%) and high oil palm (>20%) landscapes and intact [Forest Landscape Integrity Index (FLII) 7–10] *versus* degraded (FLII 0 to <7) forest landscapes.

Fig. S5. Box plots of relative abundance index (RAI) comparing between degraded [Forest Landscape Integrity Index (FLII) 0 to <7] and intact landscapes (FLII 7–10) for (A) wild boar, (B) bearded pig, (C) long-tailed macaque and (D) pig-tailed macaque.

Fig. S6. Box plots comparing relative abundance index (RAI) between landscapes with low (<1%) and high (>20%) oil palm cover for wild boar (A), bearded pig (B), long-tailed macaque (C) and pig-tailed macaque (D).

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> “And into the forest I go
>
> to lose my mind and find my soul.”
>
> *John Muir*