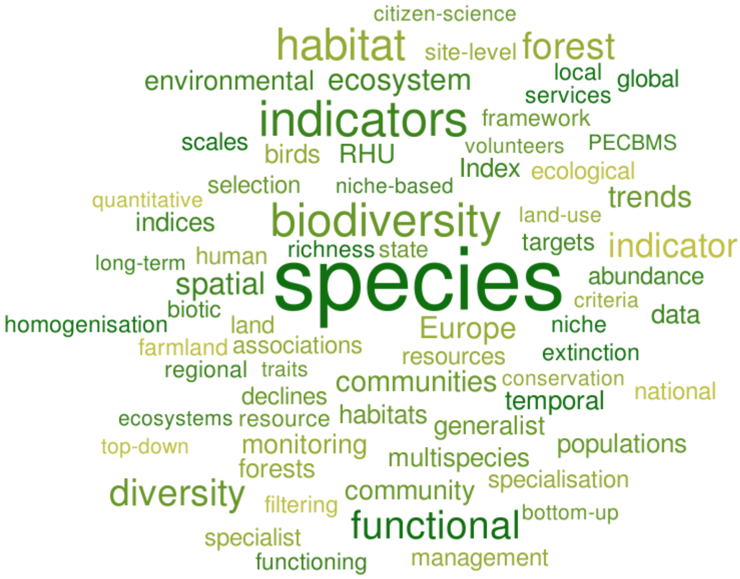
Improving and extending the use of biodiversity indicators



Thesis submitted to the School of Biological Sciences at the

University of East Anglia for the degree of Doctor of Philosophy

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December 2022

Abstract

Biodiversity indicators and indices of functional diversity can play a vital role in monitoring the impact of harmful human activity on species' populations and on the ability of biodiversity to support ecosystem functioning respectively. However, an objective, quantitative approach to indicator species selection is needed to improve the use of biodiversity indicators. Furthermore, studies suggest that conservation management should consider large-scale temporal and spatial changes in functional diversity more closely to gain a greater understanding of community functional structure.

In this thesis, I use birds as a model system to develop a fully quantitative approach to indicator species selection. I first explore a quantitative metric to determine the extent of species' habitat associations and find that literature-based classifications reflect this metric suggesting that this metric is a reliable alternative which is more robust and flexible than static literature-based classifications. I then integrate this metric with an existing niche-based framework which selects species for an indicator based on its resource use. Using this, I develop forest bird indicators for European, regional and national levels using "direct", "top-down" and "bottom-up" approaches for each. I find that for a given spatial scale, indicators produced directly at that scale ("direct") contain more sensitive species and cover more resources than an indicator produced at a higher spatial scale and adapted to lower scales ("top-down"), or an indicator produced at lower spatial scales and integrated up to produce an indicator at a higher scale ("bottom-up").

In the second half of this thesis I improve our current understanding of functional diversity indices by exploring its temporal and spatial patterns for avian communities across Europe. I find that functional diversity varies over time and space with the extent of this variation dependent on habitat and index. Finally, I extend the use of functional diversity by exploring temporal and spatial patterns in species subsets within avian communities in order to describe overall community patterns. Results show that functional diversity of the overall community is reflected in those of species subsets with the extent of this relationship varying between habitat and subset.

My research demonstrates how the use of biodiversity indicators and functional diversity indices can be improved and extended in order to make them more informative to conservation policy.

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Table of contents

Acknowledgements

First of all I would like to say a huge thank you to the thousands of volunteers from across Europe who dedicated their time throughout the past 20 years to collect the site-level data that underpinned every aspect of this PhD research. Although I only used data from 1998 to 2017, the data available runs as far as back as the 1960s! Without the time you put into collecting this data I would not be here today, so thank you!

Thank you to my supervisor, Simon Butler for giving me the opportunity to do this PhD and for your guidance and support over the past 4 and a half years. I would also like to thank my other supervisors, Richard Gregory and Lynn Dicks for their advice and help throughout my PhD.

I would like to say a special thank you to the PECBMS team; Alena Klvaňová, Eva Šilarová, Petr Voříšek and Anna Gamero for your patience and support of me and this PhD. I hope the work that I have produced can be of use to you!

I would like to thank the national coordinators who provided me with their monitoring scheme data for without this there would be no PhD!

Thank you to my co-authors on my first published data chapter and on the second (in prep) data chapter for your support of this research, for your constructive feedback and comments which have improved and strengthened the research.

I am very grateful to the support team from the High Performance Computing group at UEA for their quick email responses (!) and advice on all things cluster!

Thanks to the Strangles group for the insightful research discussions (when they happened!) but mostly for the weekly chats and occasional biscuits. Sometimes those conversations were all I needed to push on with work!

Thank you to Cat for guiding me around my first international conference, for the advice on the PECBMS data and for being quick to help whenever I dropped a random question on you!

A sincere thank you to Richard Davies for the interesting conversations and advice regarding the functional diversity chapters.

I've lived with some great people during my time in Norwich. If you can withstand a few lockdowns together then you know you're real friends! A special thank you to Chris, Elie, Leigh and Midge for everything! For the laughs, hugs, smiles, support, dinners, snacks, teas, chats, drinks, movies… You're genuinely all just the best and I honestly loved living with you all!

To the fume stack office – thank you for being such a great bunch of people to see, work alongside and eat lunch with every day! A particular thank you to the three that I started with from day one of the PhD – Midge, Harry and Kirsty. I honestly can't imagine doing this PhD alongside a more wonderful bunch. Your support, hugs and laughs have been so incredible and have helped me so many times! I don't know if I can express how much it means! Love you guys!

To Mom and Dad – it's hard to put into words how grateful I am for everything you've done for me. Thank you for your never ending support, your belief in me, always being only a phone call away when I needed you and for giving me the freedom to experience the world but always being a safety net when I needed it.

Finally to Alex – thank you for sticking with me through it all! Your patience, love, understanding and advice have helped me through some of the worst days and I'm forever grateful to you for all the support and encouragement you've given me right until the end!

Author contributions

At the time of final submission, one of four data chapters presented in this thesis is published, and one is in prep. Although I am lead author on all manuscripts, and made the largest contribution to each piece of work, I received data, help and advice from various co-authors. Author contributions are outlined below for each data chapter:

Chapter 2: Enya O'Reilly, Richard D. Gregory, Ainars Aunins, Lluís Brotons, Tomasz Chodkiewicz, Virginia Escandell, Ruud P.B. Foppen, Anna Gamero, Sergi Herrando, Frédéric Jiguet, John A. Kålås, Johannes Kamp, Alena Klvaňová, Aleksi Lehikoinen, Åke Lindström, Dario Massimino, Ingar Jostein Øien, Jiří Reif, Eva Šilarová, Norbert Teufelbauer, Sven Trautmann, Chris van Turnhout, Thomas Vikstrøm, Petr Voříšek, Simon J. Butler. **An assessment of relative habitat use as a metric for species' habitat association and degree of specialisation.** *Ecological Indicators*, https://doi.org/10.1016/j.ecolind.2021.108521.

EOR conceived the study with support from SB. EOR analysed the data and wrote the paper. SB and RDG provided feedback and advice and commented on the manuscript throughout. All other authors provided national scheme's data and commented on the manuscript.

Chapter 3: Enya O'Reilly, Richard D. Gregory, Marc Anton, Ainars Aunins, Lluís Brotons, Tomasz Chodkiewicz, Richard Coombes, Virginia Escandell, Ruud P.B. Foppen, Anna Gamero, Sergi Herrando, Iordan Hristov, Frédéric Jiguet, John A. Kålås, Johannes Kamp, Alena Klvaňová, Primož Kmecl, Aleksi Lehikoinen, Lesley Lewis, Åke Lindström, Dario Massimino, Ingar Jostein Øien, Daniel Palm Eskildsen, Jiří Reif, Benjamin Seaman, Eva Šilarová, Nicolas Strebel, Norbert Teufelbauer, Sven Trautmann, Chris van Turnhout, Thomas Vikstrøm, Petr Voříšek, Simon J. Butler. **Quantitative niche-based framework for developing biodiversity indicators: updating the European Forest Bird Indicator** (in prep.)

EOR conceived the study with support from SB. EOR analysed the data and wrote the manuscript. SB and RDG provided feedback and advice and commented on the manuscript throughout. All other authors provided national scheme's data and commented on the manuscript. ES provided European and regional species' indices and provided advice on parameters for trend production.

Chapter 4: Enya O'Reilly and Simon J. Butler. **Exploring temporal and spatial patterns of functional diversity in Europe's avian communities**

EOR conceived the study with support from SB. EOR analysed the data and wrote the chapter. SB provided feedback and advice and commented on the manuscript throughout.

Chapter 5: Enya O'Reilly and Simon J. Butler. **Using temporal and spatial patterns in functional diversity of species subsets to describe patterns in the overall avian community**

EOR conceived the study with support from SB. EOR analysed the data and wrote the chapter. SB provided feedback and advice and commented on the manuscript throughout.

Chapter One: General introduction

1.1 Biodiversity loss

Biodiversity can be defined as the total biotic variation among all living organisms and includes diversity within and between species, and of ecosystems from a single habitat to the overall biosphere (Purvis and Hector, 2000; Díaz *et al*., 2005; Reyers *et al*., 2012). Biodiversity plays a vital role in sustaining human lives by supporting goods and services and through cultural and socio-economic values (Cardinale *et al*., 2012; Turnhout *et al*., 2013). However, land use change, habitat degradation and the overexploitation of species has resulted in biodiversity loss and species' population declines within the natural world (Mace *et al*., 2018; Díaz *et al*., 2019). The Living Planet Index, which monitors the global state of biodiversity has indicated an overall 69% decline in the relative abundance of monitored wildlife populations since 1970, with declines ranging from 94% overall in Latin America and the Caribbean to 18% in Europe and Central Asia (WWF, 2022). These biodiversity declines have been exacerbated by humans placing ever increasing pressure on biodiversity and ecosystems to provide energy, food and other services in order to fuel economic growth and support growing human populations (Díaz *et al*., 2019; IPBES, 2019; Pascual *et al*., 2021; WWF, 2022).

1.2 Importance of biodiversity indicators

Population declines and threats to biodiversity have led to actions at a governmental level to develop initiatives and targets which aim to reduce these biodiversity declines (Mace *et al*., 2018). In 1992, the Convention on Biological Diversity (CBD) was adopted as the first global agreement between the world's national governments that was focused on a united approach to conserving and sustainably using biodiversity (Secretariat of the Convention on Biological Diversity, 2000). To monitor progress towards reducing the rate of biodiversity loss, a number of targets were set in 2002 to be achieved by 2010 (Secretariat of the Convention on Biological Diversity, 2002; Heink and Kowarik, 2010), and further targets in 2010 to be achieved by 2020

(CBD, 2010). Progress towards these targets were measured at local, regional and global levels using a suite of indicators which tracked biodiversity trends at the genetic, species, population and ecosystem levels (CBD, 2010; Walpole *et al.*, 2009). Unfortunately studies have found that based on these indicators the targets were not met in full by 2010 or 2020 (Butchart *et al*., 2010; Buchanan *et al*., 2020). At the time of writing, the CBD are meeting again to produce a new set of ambitious post-2020 targets that aim to reduce biodiversity loss and ensure its sustainable use by 2050. Biodiversity indicators will once again play a pivotal role in this post-2020 framework to monitor progress towards local, regional and global targets (CBD, 2022).

Early references to biodiversity indicators date back to the 1910s when plant communities were monitored to indicate changes in soil conditions (Rapport, 1992) and caged canaries gave early warning signals to coal miners of the presence of poisonous gases in mines (Burrell and Siebert, 1916; Niemi and McDonald, 2004; Gregory and Strien, 2010). Today, biodiversity indicators communicate results of population trends for single or multiple species as a metric value (Quinn *et al*., 2011). From this, we can establish environmental baselines and assess conditions relative to this baseline through temporal and spatial trends (Dale and Beyeler, 2001). Outcomes from these trends can be used to simplify the complexities of ecosystem functioning and explain the impact of anthropogenic activities and climate change on species and ecosystems (Scheffer *et al*., 2001; Dale and Beyeler, 2001; Gregory *et al*., 2009). Furthermore, biodiversity indicators can be easily interpreted for the general public and used within policies and governmental reports (Gregory *et al*., 2005; Niemeijer and de Groot, 2008) to prioritize conservation efforts and revise management strategies (Hunter *et al*., 2016).

At the species level, a variety of potential indicators have been suggested (Lambeck, 1997; Noss, 1999), including umbrella species *i.e.*, which require large areas of suitable habitat to sustain viable populations and whose requirements are similar to those needed by an array of other species (Fleischman *et al.*, 2001), and flagship species which have large public appeal as they are often charismatic megafauna (Niemi and McDonald, 2004). However, a single species or population is unlikely to accurately reflect the multiple dimensions of species diversity in an ecosystem (Lambeck, 1997). Furthermore, single species indicators overlook more common species which can represent the overall state of nature (Gregory *et al.*, 2005). For these reasons, multispecies indicators are a more widely accepted and favoured approach by researchers (Maes, 2005; Gregory and Strien, 2010).

Multispecies indicators can be defined as a group of species whose population trends, when taken together, reflect the average behaviour of the constituent species to environmental changes. They represent the reaction of other, unmonitored species to human disturbance, thereby acting as a reliable proxy for overall ecosystem health (Caro and O'Doherty, 1999; Gregory *et al*., 2005). For example, the Biodiversity Intactness Index provides information on the state of biodiversity in a given area in response to a set of land use activities (Scholes and Biggs, 2005), and the Red List Index measures changes in extinction risk for an aggregate suite of species to give an overall depiction of extinction rate of biodiversity (Butchart *et al*., 2004, 2007). In addition, the Biodiversity Change Index monitors changes in the quantity and quality of overall change in biodiversity by tracking changes in the area of a specified habitat and the abundance of indicator species in that habitat (Normander *et al*., 2012).

1.3 Contribution of citizen science data to biodiversity indicators

In order to produce multispecies indicators and monitor species' populations across broad spatial scales, detailed, large-scale monitoring data are needed (Kelling *et al*., 2015). Long-term monitoring is the act of continuously collecting field-based empirical measurements and analysing this information for at least 10 years (Lindenmayer and Likens, 2010). As governments and scientific agencies lack the resources to support long-term biodiversity monitoring by scientists, many organisations recruit volunteers to carry out surveys (Kelling *et* *al*., 2019). It is estimated that up to 85% of all species level information required by governments globally are collected by these volunteers or citizen scientists (Roy *et al.*, 2012) and citizen science monitoring programmes have contributed to tracking large-scale changes in plant, butterfly, coral reef and bird indicators (Pescott *et al*., 2015; Lau *et al*., 2019; Van Swaay *et al*., 2019; Brlík *et al*., 2021). For example, volunteers have helped to monitor and identify the locations of global coral bleaching events (Marshall *et al*., 2012) and track the impact of climate warming on development timings of common plants in Canada (Beaubien and Hamann, 2011). The largest and longest running citizen science programs are bird monitoring schemes such as the National Audubon Society's Christmas Bird Count in the United States which began in 1900 (Tulloch *et al*., 2013). In addition, in Europe, volunteers and scientists have collected site-level bird count data as part of national level monitoring schemes since the 1980s (Brlík *et al*., 2021). These data have been collated under the Pan-European Common Bird Monitoring Scheme (PECBMS) which was specifically set up to monitor bird population trends and progress towards the CBD 2010 targets (Gregory, 2006).

1.4 Birds as a model system for biodiversity indicators

Birds are generally viewed as reliable biodiversity indicators due to their sensitive and predictable response to anthropogenic and natural environmental changes (Järvinen and Väisänen, 1979). Surveying birds is also relatively straightforward as they are easy to identify and collecting count data on birds is inexpensive due to the number of long-term citizen science monitoring schemes for birds (Pereira and David Cooper, 2006; Gregory and Strien, 2010; Eglington *et al*., 2012; Furness and Greenwood, 2013; Fraixedas *et al*., 2020). They are also widespread and diverse and live in most terrestrial and aquatic habitats across all continents, making their populations comparable across broad spatial scales (Gregory *et al*., 2005; Gregory and Strien, 2010). For example, the North American Bird Wintering Ranges Index has monitored the impact of climate change on bird behaviour and their wintering ranges since the

1960s (National Audubon Society, 2009) and the European Wild Bird Indices have monitored the general state of breeding bird populations in Europe since the 1980s (Brlík *et al*., 2021; Gregory *et al*., 2019). The European Wild Bird Indices, produced by the PECBMS, include multispecies indicators for two predominant habitats in Europe - farmland and forest, which have been subject to extensive human modification and exploitation over recent decades (Gregory et. al., 2005; Fraixedas *et al*., 2020). Most notably, the Farmland Bird Index has tracked a steady decline in farmland bird populations with an increase in agricultural intensification over the past four decades (Donald *et al*., 2001; Brlík *et al*., 2021).

Caution is often taken when drawing conclusions from bird indicator trends due to questions that are raised over how faithfully a single taxon can represent the status and trends of other taxa (Gregory and Strien, 2010). For example, a UK study found that within the same time frame, plant, bird and butterfly populations all declined, but butterfly populations declined more than the others (Thomas *et al*., 2004). Furthermore, some bird species can respond positively to anthropogenic change while others will not. Despite these caveats, birds are viewed as the best indicators for the general state of biodiversity that are currently available (Gregory, 2006).

1.5 Biodiversity indicators in forest habitat

Forests cover 31% of the global land area and directly support 33 million people working in the forestry sector. Furthermore, it is estimated that 21% of the total wealth in land assets and 9% of the world gross domestic product come from ecosystem services directly supplied by forests such as recreation, habitat, hunting and water services. As well as this, forests provide essential habitat for 80% of amphibian, 75% of bird and 68% of mammal species globally, not to mention act as a vital carbon storage system, with forests containing 662 billion tonnes of carbon (*The State of the World's Forests*, 2022). Despite their importance, forest land area is declining globally with 420 million hectares lost through deforestation between 1990 and 2020. Interestingly, forest area is not declining evenly across the globe (FAO, 2020). The highest net losses between 2010 and 2020 occurred in South America and Africa, while Europe (Forest Europe, 2020) and parts of Asia showed net gains within that time (FAO, 2020). However, losses in the tropics outweigh gains in other parts of the globe (Song *et al*., 2018).

At the Rio Earth Summit in 1992 it was recognised that global forest resources are essential for the conservation of biodiversity, water and soil resources and for basic human requirements. Since then a number of criteria and biodiversity indicators for forests have been developed under the CBD, within Forest Europe and as part of the Montreal Process in order to monitor success towards achieving sustainable forest management and safeguard the future of its resources (Siry *et al*., 2005). Indicators are a key component of sustainable forestry management as they allow land managers and policy makers to understand the impact of management treatments and disturbances on the composition and structure of forests and how this will effect biodiversity (Noss, 1999; Bengtsson *et al*., 2000; Lindenmayer *et al*., 2000; Torras and Saura, 2008; White *et al*., 2015). Due to ongoing natural disturbances (Schurman *et al*., 2018), pressures from climate change (Seidl *et al*., 2020) and political challenges (Sotirov *et al*., 2021) putting greater pressure on forest ecosystems and provision of ecosystem services, Forest Europe, who are central to European policy for sustainable forest management (Forest Europe, UNECE and FAO, 2011), recently set out to revise and update its European forest indicators. In addition, evidence showed that a revised forest strategy and framework was needed to account for regional differences in forests across Europe (European Commission, 2013).

1.6 Indicator species selection approaches

Since it is not feasible to monitor all species within an ecosystem, choosing which species to monitor is of critical importance when developing biodiversity indicators (Hilty and Merenlender, 2000; Lindenmayer *et al*., 2000; Carignan and Villard, 2002; Fraixedas *et al*., 2020). However, this is often not straightforward as a number of different approaches exist for choosing indicator species (Hilty and Merenlender, 2000) which can be based on expert knowledge (Gregory *et al*., 2005), past research, ecological importance, species' abundance or a combination of these methods (Siddig *et al*., 2016). Furthermore, indicator species choice can have repercussions for the types of management decisions that are made (Grantham *et al*., 2010). Therefore, in order to be informative, indicators should include species which meet a set number of criteria (Table 1.1) (Carignan and Villard, 2002; Gregory *et al*., 2005; Gregory and Strien, 2010).

Table 1.1. Key attributes of an effective biodiversity indicator (Gregory and Strien, 2010).

Attribute	Details
Representative	Includes all species in a taxon or representative group
Immediate	Can be regularly updated
Simplifying	Reduces complex information into accessible form
Easily understood	Simple and transparent
Quantitative	Accurate measurement with assessment of precision
Responsive to change	Sensitive to environmental change over short time scales
Timeliness	Allows early warning of issues
Susceptible to analysis	Data can be disaggregated to understand underlying patterns
Realistic to collect	Data can be collected within resources and finance over medium to long term
Indicative	Representing more general components of biodiversity

User driven	Developed in response to policy needs
Policy relevant	Allow policy makers to develop and adapt instruments
Stability	Buffered from highly irregular natural fluctuations
Tractable	Susceptible to human influence and change

Studies have found that indicator species selection approaches which adopt specific selection criteria to identify the potential indicator species pool are more representative of the wider community (Butler *et al*., 2012; Wade *et al*., 2014; Fraixedas *et al*., 2020). For example, studies have demonstrated means of quantifying species' habitat associations and determining their habitat preferences based on data collected through monitoring schemes (Larsen *et al*., 2011; Jiguet *et al*., 2012; Renwick *et al*., 2012; O'Reilly *et al.*, 2022). Furthermore, studies have produced multispecies indicators using a niche-based framework whereby species are systematically chosen for an indicator based on their resource requirements, so any change in resource availability will be detected by trends in the indicator (Butler *et al*., 2012; Wade *et al*., 2014). Further approaches for choosing indicator species involve ordination methods which associate species with habitat types based on different environmental characteristics (Kremen, 1992) or identify species that have the highest potential as indicators within a community and habitat (Dufrêne and Legendre, 1997). Additional methods are available which choose a ratio of species for an indicator that are positively and negatively affected by an environmental driver, thereby allowing a greater understanding of patterns affecting indicator trends (Herrando *et al*., 2016; Stephens *et al*., 2016).

An additional concern in indicator species selection is the scale at which indicators should be selected in order to provide reliable advice to policy-makers and land managers (Flather *et al*., 1997; Hess *et al*., 2006). For example, "top-down" indicators are produced at large spatial scales and adopted at regional and national levels. However, these may be insensitive to spatial differences in species' habitat associations due to spatial variation in habitat-biodiversity relationships (Knight and Cowling, 2007). Alternatively, "bottom-up" indicators take species' habitat associations at the local scale into consideration and then aggregate and project these indicators up to larger spatial scales (Fraser *et al.*, 2006; Feld *et al.*, 2009). Due to spatial differences in survey coverage, it may however not be feasible to collect sufficient and reliable data across all local scales for a "bottom-up" indicator (Roux *et al.*, 2016). "Direct" indicators may therefore be an alternative option as they use species' habitat associations at a given spatial scale to produce multispecies indicators for that same scale (Feld *et al.*, 2009; Terrigeol *et al.*, 2022). However, it may be challenging to compare "direct" indicators across spatial scales if the same species are not used (Remme *et al.*, 2016).

1.7 Metrics for habitat specialisation

Determining species specialisation to a habitat is a key factor in understanding species' extinction risk (Colles *et al.*, 2009), in producing biodiversity indicators and monitoring species' response to environmental changes (Butler *et al.*, 2007; Clavel *et al.*, 2011) and in designing appropriate conservation strategies (Poisot *et al.*, 2012). For example, specialist species are at higher risk of population declines or extinction as they occupy a smaller niche space *i.e.*, use a restricted range of habitats or only use a portion of the resources that are available in a habitat (Julliard *et al.*, 2006; Morelli *et al.*, 2019). Furthermore, they have low dispersal capabilities and are less efficient in coping with environmental variations (McKinney and Lockwood, 1999; Colles *et al.*, 2009; Devictor *et al.*, 2010). Due to their sensitivity to environmental changes biodiversity indicators often include specialist species to ensure that the indicator is sensitive to changes (Gregory *et al.*, 2005; Devictor *et al.*, 2010; Vimal and Devictor, 2015). In contrast, generalist species have a larger niche breadth *i.e.*, are capable of surviving in a range of habitats, utilise a wide variety of resources (Futuyma and Moreno, 1988;

Julliard *et al.*, 2006; Morelli *et al.*, 2019) and are more resilient to environmental changes (Devictor *et al.*, 2008).

Species' specialisation classifications are often categorical *i.e.*, specialist or generalist (Fridley *et al.*, 2007; Devictor *et al.*, 2008, 2010; Chazdon *et al.*, 2011; Morelli *et al.*, 2019) with classifications assigned based on expert opinions, small scale field studies or observations (Thogmartin and Knutson, 2007; Redhead *et al.*, 2016). However, in recent decades researchers have recognised that species are more likely to sit along a gradient of specialist to generalist dependent on their affinity to a habitat and their niche breadth (Devictor *et al.*, 2010; Clavel *et al.*, 2011; Morelli *et al.*, 2019). A number of metrics have therefore been developed to quantify species' specialisation to a habitat. These include Simpson's and Shannon's Diversity Indices (Levins, 1968), Species Specialisation Index (SSI) (Julliard *et al.*, 2006; Devictor *et al.*, 2008) and Relative Habitat Use (RHU) (Larsen *et al.*, 2011).

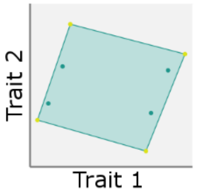
Studies have reported that human-induced land use change and habitat degradation are causing more significant declines and higher rates of extinction in specialists compared to generalists and that community composition is shifting towards an increase in generalist species and away from specialist species (McKinney, 1997; Colles *et al.*, 2009; Devictor *et al.*, 2010; Clavel *et al.*, 2011). This replacement of species specialised to a given habitat with generalist species that are more widespread and occupy a larger range of habitats is referred to as biotic homogenisation as communities become spatially less diverse (McKinney and Lockwood, 1999; Olden *et al.*, 2004; Clavel *et al.*, 2011). Biotic homogenisation can be referred to as taxonomic or functional homogenisation (Olden and Rooney, 2006). Taxonomic homogenisation refers to the increased similarity in species composition between communities, while functional homogenisation can be defined as the increase in functional similarity of communities, with generalist species often fulfilling similar functional roles and occupying similar ecological niches over time (Olden *et al.*, 2004; Olden and Rooney, 2006; Clavel *et al.*, 2011). Therefore, an increase in the number of generalist species and declines in the diversity and abundance of specialist species may have a significant effect on ecosystem functioning (Clavel *et al*., 2011).

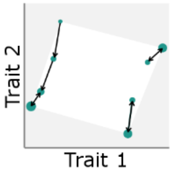
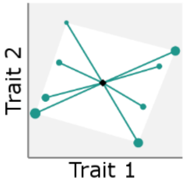
1.8 Indices of functional diversity for monitoring ecosystem functioning

Increased ecosystem functioning is related to greater resource use complementarity and ecosystem service provision, *e.g.,* pest and disease control, soil and water regulation and pollination, among species in a local community (Tilman, 1997; Hooper, 1998; Loreau, 1998, 2001; Petchey *et al*., 2004). This concept is closely related to niche theory which finds that separation of niche space in a community allows greater coexistence among species due to lack of competition for similar resources (Macarthur and Levins, 1967; Clavel *et al*., 2011). In the recent Dasgupta, (2021) report on the economics of biodiversity, he comments that ecosystem's productivity and resilience to land-use change relies less on a community's taxonomic diversity or species richness, and more so on the range of functions played by species in a community. Therefore studying the functional diversity of ecological communities allows us to move beyond simple indices, such as species richness and increase our understanding of community assembly processes (Tilman, 1997; Mouillot *et al*., 2007; Cadotte *et al*., 2011; Mason *et al*., 2012; Díaz *et al*., 2013), communities response to environmental changes (Mouillot *et al*., 2013) and can act as a predictor of ecosystem functioning (Díaz and Cabido, 2001; Díaz *et al*., 2006; Roscher *et al*., 2012).

Functional diversity describes differences between species in a community (Tilman, 2001) by measuring the range, abundance and distribution of species' functional traits (Petchey and Gaston, 2006; Mason *et al*., 2012), with functional traits providing key information on a species' ecological niche (Petchey and Gaston, 2002; Villéger *et al*., 2008; Pigot *et al*., 2020; Stewart *et al*., 2022). The functional structure of ecological communities are composed of multiple, independent aspects (Mason *et al*., 2005; Mouchet *et al*., 2010) which a single index cannot compute (Mouillot *et al*., 2013). Therefore, a range of indices have been developed which each quantify slightly different aspects of functional diversity (Mason *et al*., 2005) (Table 1.2). Functional diversity studies have contributed to developing a greater understanding of assembly rules driven by species' functional traits (Mason *et al*., 2007; Mouillot *et al*., 2007). From these studies, three filtering processes have been identified which shape community structure. Abiotic filtering, which is often felt most strongly at large spatial scales (Díaz *et al*., 1999; Cornwell *et al*., 2006), selects for species that are more functionally similar than expected by chance. This is due to environmental conditions acting as a filter and limiting the range of functional traits in a habitat (Mouchet *et al*., 2010). In comparison, biotic filtering selects for functionally dissimilar species as competitive exclusion and resource partitioning limits the functional similarity between species (Macarthur and Levins, 1967; Purschke *et al*., 2013). Biotic filtering is more likely to drive local assembly patterns due to species interactions at the site level (Cavender-Bares *et al*., 2004; Slingsby *et al*., 2006). However, abiotic and biotic filtering are not mutually exclusive (Laliberté *et al*., 2013). Finally, neutral theory assumes that all species are ecologically identical and therefore that communities are randomly assembled (Hubbell, 2001). This assumption allows studies to compare functional diversity to a null distribution of species predicted by neutral theory, with species richness held constant (Flynn *et al*., 2009; Mendez *et al*., 2012; Chalmandrier *et al*., 2013; Mason *et al*., 2013).

Table 1.2. Examples of functional diversity indices developed in recent decades and used in this study. To further explain how each index is calculated, an exemplary simulated community is plotted in two-dimensional functional trait space according to two traits. In the context of this study, community can be described as the group of species at a given site, in a given year. Species' distances from one another were extracted from a Principal Coordinates Analysis (PCoA). In the context of the functional richness index, yellow circles represent species on the boundaries of functional trait space. For functional evenness, dispersion, originality and specialisation, circle sizes are proportional to species' relative abundances, and for functional originality, arrows show the direction of each species to its nearest neighbour. The final column illustrates how each functional diversity index for the simulated community could increase or decrease.

Functional diversity index	Definition	Simulated example	Index response
Functional richness (FRic) (Villéger *et al.*, 2008)	Describes the amount of functional trait space occupied by species in a community.		• Increases if a functionally unique species appears in the community. • Decreases if one of the existing species on the boundary of trait space disappears from the community.
Functional evenness (FEve) (Villéger *et al.*, 2008)	Describes the regularity with which species' abundances are distributed in functional trait space (along the shortest minimum spanning tree linking all species).		• Increases as species' abundances become more similar. • Decreases as the abundance of one species becomes more dissimilar to all other species in the community.

Functional dispersion (FDis) (Laliberté and Legendre, 2010)	Describes the mean distance of individual species to the centroid of all species in multidimensional trait space, weighted by species' relative abundances.		• Increases if species' abundances in the upper left or right corners increase, as the centroid will be more central to all species. • Decreases if species' abundances in the lower left or right corners increase, as the centroid is pulled towards the more abundant species.
Functional originality (FOri) (Mouillot *et al.*, 2013)	Describes the weighted mean distance of each species to its nearest neighbour in functional trait space. Distances are weighted based on species' relative abundances. Describes the isolation of a species in the functional trait space of a community.		• Increases if a functionally unique species appears in the community. • Decreases if a functionally similar species appears in the community, or if the relative abundance of one of the existing species compared to its nearest neighbour increases.
Functional specialisation (FSpe) (Mouillot *et al.*, 2013)	Describes the mean distance of a species from the rest of the species pool in functional space.		• Increases as relative abundance of functionally unique species (far from centroid) compared to that of functionally similar (close to centroid) species increases. • Decreases as the relative abundance of functionally similar (close to centroid) species compared to that of functionally unique (far from centroid) species increases.

1.9 Thesis structure

In this thesis, annual, site-level count data for European breeding birds collected by national level monitoring schemes and collated by the PECBMS are used to explore two primary objectives; i) improve the species selection approach to biodiversity indicators using quantitative methods and ii) explore large-scale temporal and spatial patterns in functional diversity indices to shed further light on potential assembly processes that shape the functional composition of avian communities in Europe.

Species selection for biodiversity indicators often relies on expert opinion (Gregory *et al*., 2005, 2008; Forest Europe, 2019) or literature-based classifications (Siddig *et al*., 2016). However this approach risks introducing bias or subjectivity to the selection process due to individual expert opinions (Forest Europe, 2019; Gregory *et al*., 2019) or may fail to account for spatial variation in the extent of species' habitat associations (Reif *et al*., 2008). Quantitative metrics are available to objectively select species for an indicator based on the extent of their habitat associations (Larsen *et al*., 2011; Jiguet *et al*., 2012; Renwick *et al*., 2012; Fraixedas *et al*., 2020). Therefore, in **Chapter two**, I explore one of these quantitative metrics, Relative Habitat Use (RHU) (Larsen *et al*., 2011) as a metric for quantifying species' habitat association and degree of specialisation. For this, I first assess the relationship between RHU and existing categorical classifications of species' habitat associations derived from the literature. I then assess the performance of RHU in quantifying degree of habitat specialisation by comparing RHU scores for species reported in the literature as only associated with one habitat, *i.e.,* specialist species to those reported in the literature as associated with more than one habitat, *i.e.,* generalist species. Finally, I examine the stability and consistency in RHU scores by assessing temporal variation in RHU.

Using my exploration of RHU from the first chapter, in **Chapter three** I integrate RHU and the niche-based framework proposed by Butler *et al.*, (2012) to produce a quantitative and objective approach to indicator species selection for an updated European Forest Bird Indicator. I focus on Europe's forest birds in this chapter as Forest Europe have specified that given mounting environmental and political pressures on European forests, they seek to revise and potentially update the indicators, including the current Forest Bird Indicator (Forest Europe, 2019). Currently, the niche-based framework relies to some extent on expert-based opinions when producing multispecies indicators as they are used to determine the candidate species pool from which indicator species are selected and are used to quantify the extent of species' reliance on the target habitat (Butler *et al.*, 2012; Wade *et al.*, 2014). In this third chapter, I therefore replace these expert-based opinions with RHU to systematically choose the candidate species pool and quantify each species' reliance on forest habitat. In chapter three, I also aim to explore the implications for species composition and indicator trends if a "direct", "top-down" or "bottom-up" approach is taken to producing multispecies indicators. I explore this by developing multispecies indicators for forest birds using the integrated niche-based framework at "direct", "top-down" and "bottom-up" approaches at national, regional and European levels. I then compare the average sensitivity, resource coverage and temporal trends between indicator sets generated for each spatial scale using the different approaches and discuss differences between them.

Temporal and spatial patterns in species richness, abundance and turnover have long been explored in ecological studies to monitor the effects of human activity, land-use change and conservation management on biodiversity (Soininen, 2010; Hendershot *et al.*, 2020; Pellissier *et al.*, 2020; Floigl *et al.*, 2022). Biodiversity indicators, such as those explored in chapter two and three are beneficial as they monitor population changes of particular suites of species that are highly reliant on a target habitat. In the latter two chapters of the thesis, I explore temporal and spatial patterns in functional diversity for avian communities in Europe as studies have shown that changes in biodiversity are positively related to changes in ecosystem function (Petchey and Gaston, 2006; Mouchet *et al.*, 2010). Similar to multispecies indicators, trends in functional diversity can uncover more nuanced changes in ecosystem health and stability, and ability to provide ecosystem services.

In **Chapter four** I use the site-level bird count data to explore temporal and spatial patterns in five functional diversity indices; functional richness (FRic), evenness (FEve), dispersion (FDis), originality (FOri) and specialisation (FSpe) for European breeding bird communities in five broad habitat types that dominate the European landscape; forest, farmland, urban, wetland and semi-natural. I compare temporal trends across habitats for each index to determine if there are differences between habitats and compare site-level trends across Europe to determine if there are latitudinal and/or longitudinal patterns in functional diversity. Finally, I compare site-level trends in species richness, total abundance and functional diversity to determine if the former two are correlated with functional diversity.

To further understand underlying patterns in avian community structure I focus, in **Chapter five**, on functional diversity in forest and farmland, as these habitats have experienced significant human modification in recent decades (McElhinny *et al.*, 2005; Tscharntke *et al.*, 2005). As a result of land-use change and habitat degradation, ecological communities are shifting away from specialists and towards a greater diversity and abundance of generalist species (Julliard *et al.*, 2006; Smart *et al.*, 2006; Devictor *et al.*, 2008; Clavel *et al.*, 2011; Ibarra and Martin, 2015) and potentially an increase in habitat visitors, as habitats become more fragmented (Jones *et al.*, 2005). If these patterns continue, community functional diversity may decline as species become functionally more similar, which can have a negative effect on ecosystem service provision. Therefore in chapter five I explore temporal trends in forest and farmland functional diversity for the full avian community and use patterns in species subsets;

generalists, specialists and visitors, to understand the mechanisms that may drive them. I also explore temporal and spatial patterns in species subsets using a null model approach to determine if observed functional diversity indices differ from those expected based on random simulated communities over time and across latitudinal and longitudinal gradients.

Finally, in **Chapter six** I draw some general conclusions from across the thesis.

Chapter Two: An assessment of relative habitat use as a metric for species' habitat association and degree of specialisation

2.1 Abstract

In order to understand species' sensitivity to habitat change, we must correctly determine if a species is associated with a habitat or not, and if it is associated, its degree of specialisation for that habitat. However, definitions of species' habitat association and specialisation are often static, categorical classifications that coarsely define species as either habitat specialists or generalists and can fail to account for potential temporal or spatial differences in association or specialisation. In contrast, quantitative metrics can provide a more nuanced assessment, defining species' habitat associations and specialisation along a continuous scale and accommodate for temporal or spatial variation, but these approaches are less widely used. Here we explore relative habitat use (RHU) as a metric for quantifying species' association with and degree of specialisation for different habitat types. RHU determines the extent of a species' association with a given habitat by comparing its abundance in that habitat relative to its mean abundance across all other habitats. Using monitoring data for breeding birds across Europe from 1998-2017; we calculate RHU scores for 246 species for five habitat types and compared them to the literature-based classifications of their association with and specialisation for each of these habitats. We also explored the temporal variation in species' RHU scores for each habitat and assessed how this varied according to association and degree of specialisation. In general, species' RHU and literature-derived classifications were well aligned, as RHU scores for a given habitat increased in line with reported association and specialisation. In addition, temporal variation in RHU scores were influenced by association and degree of specialisation, with lower scores for those associated with, and those more specialised to, a given habitat. As a continuous metric, RHU allows a detailed assessment of species' association with and degree of specialisation for different habitats that can be tailored to specific temporal and/or spatial requirements. It has the potential to be a valuable tool for identifying indicator species and in supporting the design, implementation and monitoring of conservation management actions.

2.2 Introduction

There is growing recognition that continued biodiversity declines and loss of species through land-use change and habitat degradation are occurring in a non-random manner, with specialist species' populations declining at faster rates compared to generalist species (Devictor *et al.,* 2010). Accurately assessing species' specialisation is therefore vital to better understand their potential sensitivity to changes in the quantity or quality of available habitat and their vulnerability to population declines. However, assessments of specialisation are often categorical, with species grouped into those that are associated with or are not associated with a given habitat, and whether those that are associated are habitat specialists or generalists (Fridley *et al.,* 2007; Devictor *et al*., 2008, 2010; Chazdon *et al.,* 2011; Herrando *et al.,* 2016; Morelli *et al*., 2019). Specialism itself is also characterised in two dimensions - specialist species are defined as those whose populations are restricted to a smaller range of habitats and/or use a small portion of the resources that are available in a habitat (Reid *et al.,* 2005; Smart *et al.*, 2006; Devictor *et al.*, 2008). By comparison, generalist species are defined as those that are capable of exploiting a range of habitats, and/or use a larger number of the available resources in a habitat (Morelli *et al.,* 2019); here we focus on definitions of specialisation that are based on the range of habitats a species uses rather than resource use within habitats. Assessments of habitat association and specialisation are often derived from expert opinions, observations or small-scale field studies (Thogmartin and Knutson, 2007; Redhead *et al.*, 2016), and are generally applied at the species level. As a result, phenotypic plasticity in response to temporal and spatial changes in environmental conditions, which may cause variation in a species' realized niche and therefore in its association with and specialisation for a given habitat, can be overlooked (Devictor *et al.,* 2010). In addition, categorical classifications that simply define a list of species as specialised to a given habitat fail to acknowledge that there is variation between species in their degree of specialisation for that habitat, and that this may have an important effect on their population trends over time (Reif *et al.,* 2008).

A number of quantitative metrics that can account for temporal and spatial variation in association and specialisation and allow between-species comparisons have been proposed (Julliard *et al.,* 2006; Devictor *et al.,* 2008; Reif *et al.,* 2008; Larsen *et al.,* 2011; Renwick *et al.,* 2012; Rivas-Salvador *et al.,* 2019). Simple metrics such as Simpson's and Shannon's Diversity Indices (Levins, 1968), which follow Levins' measure of niche breadth, quantify specialisation as the number of habitats used by a species, relative to the total number of habitats available (Levins, 1968). These metrics are both easy to explain and calculate and can accommodate presence/absence or abundance data (Devictor *et al.,* 2010). However, they can be subject to sampling biases and limitations, particularly as both indices calculate specialisation on the assumption that all habitats are equally available (Petraitis, 1979). Julliard *et al.* (2006) presented an alternative approach, the Species Specialisation Index (SSI), which quantifies species' degree of specialisation for a given habitat as the coefficient of variation (standard deviation/mean) in species' abundance across habitats. Low SSI scores infer that there is little variation in a species' abundance between habitats, and that the species is more general in its habitat use, while high SSI scores imply that a species has a high abundance in a limited number of habitats and is therefore more specialised (Julliard *et al.,* 2006; Devictor *et al.,* 2008). This approach minimises the limitations of Simpson's and Shannon's Indices by avoiding the assumption that habitats are equally available (Hayward *et al.,* 2006; Julliard *et al.,* 2006). However, SSI only gives a single score per species, defining its overall degree of specialisation rather than its specialisation for individual habitats (Julliard *et al.,* 2006; Reif *et al.,* 2010). Furthermore, while SSI calculates specialisation based on variation in species' abundance across habitats, this can present limitations if based on only a small number of sites for that habitat or if there are differences in sample size of sites between habitats (Morelli *et* *al.,* 2019). Renwick *et al.* (2012) provide an alternative to SSI that accounts for the sample size of sites by adapting Jacobs' Preference Index (Jacobs, 1974), which determines species' specialisation for a habitat by comparing the proportion of habitat used to the proportion of habitat available. Jacobs' Index does not account for species' abundances across habitats, but Renwick *et al.* (2012) adapted the index by comparing species' counts on sampled transects in sites of a target habitat to species' counts that would otherwise be found from random surveying of sites. Species with a significantly higher proportion of counts in sites of the target habitat were classified as being specialised to that habitat. Whilst accounting for the number of sites sampled improves on SSI, Renwick *et al.*'s (2012) approach still only allows us to determine if a species' is specialised or not to a habitat of particular interest. It is not calculated in such a way that allows us to explore the extent of species' specialisation for each individual habitat.

The relative habitat use (RHU) metric was introduced by Larsen *et al.* (2011) as an alternative approach to quantifying species' habitat association and degree of specialisation. RHU is derived from the SSI measure but is computed for each habitat in turn, allowing for cross-habitat comparisons. Specifically, it measures a species' association with a given habitat as its abundance in that habitat relative to its mean abundance in all other habitats, accounting for both the total number of sites and the number of sites of that specific habitat surveyed. An RHU score of less than one infers a weak association with a habitat, one to two as a moderate association, and greater than two as a strong association with the habitat (Eskildsen *et al.,* 2013). The number of habitats a species is identified as having an association with (RHU ≥ 1) indicates its degree of habitat specialisation. This metric can be calculated at any temporal and/or spatial scale, allowing comparisons in RHU scores to be made across time and space. Larsen *et al.* (2011) applied this approach to the Danish avifauna, identifying sets of specialist forest birds and farmland birds that differed to those derived from categorical-based assessments that relied on expert opinions. The index for forest habitat based on the RHU approach saw an overall negative trend, while the index for the categorical-based approach remained stable over time.

In this paper, we explore the performance of RHU as a metric for quantifying species' habitat association and degree of specialisation more generally and explore variation in species' RHU scores over time. First, we assess the relationship between RHU and existing categorical classifications of species' habitat associations that are derived from the literature. We predict that species' RHUs should be higher for those habitats that they have been reported in the literature as being associated with than those habitats with no reported association. Second, we assess the performance of RHU in quantifying degree of habitat specialisation by comparing RHU scores for more specialist species *i.e.,* those reported in the literature as only being associated with one habitat to more generalist species *i.e.,* those reported in the literature as being associated with that habitat plus one or two others, hypothesising that species more specialised to a given habitat will have a higher RHU for that habitat than more generalist species. We then assess the influence of habitat association and degree of specialisation on temporal variation in RHU scores to examine its stability and consistency.

We use long-term monitoring data for breeding birds across Europe, collected and collated under the Pan-European Common Bird Monitoring Scheme (PECBMS: https://pecbms.info/about-us/; Brlík *et al.,* 2021), to calculate RHU scores for each species. Birds are commonly used as indicator species due to their sensitivity to environmental changes and well-studied ecology, physiology and behaviours (Gregory *et al.,* 2005; BirdLife International, 2020). PECBMS data are used to produce i) individual species population trends at Pan-European levels, and ii) multi-species composite indices for all common bird species, and for subsets of species categorized as being associated with forest and farmland habitats (Gregory *et al.,* 2005; Gregory *et al.,* 2019). These indices in turn support EU biodiversity targets across national, regional, and European spatial scales (EEA, 2012; Fraixedas *et al.,* 2020), and can be used to monitor the effects of management practices on bird species (Wade *et al.,* 2013, 2014; Gamero *et al.,* 2017). Objectively quantifying the extent of species' association with and degree of specialisation for different habitats could advance our understanding of individual species' vulnerability to environmental changes and management practices. Furthermore, these metrics could be used to underpin the selection of species for inclusion in multi-species indicators, for monitoring biodiversity health and measuring progress towards biodiversity conservation targets (Pereira and Cooper, 2006; Niemeijer and de Groot, 2008; Walpole *et al*., 2009; Larsen *et al*., 2011).

2.3 Methods

2.3.1 Count data

We use annual, site-level count data for breeding birds from 19 monitoring schemes in 17 countries across Europe collated by PECBMS. In each scheme, species are surveyed using one of three possible techniques; point count, line transect or territory mapping (Brlík *et al.*, 2021). The geographical coordinates of the centroids of each survey site (22,710 sites in total) are known, with count data from 1998 to 2017 used here to ensure coverage from a representative suite of countries. Of the 426 species recorded by the national monitoring schemes during this period, we removed introduced species *i.e.,* those introduced outside of its historical distribution range through direct or indirect human activity (23), and locally specific species *i.e.,* those only found in a small area of one country (7). Subspecies were grouped at species level (Handbook of the Birds of the World and BirdLife International, 2020).

2.3.2 RHU calculation

We extracted Level three habitat data from Corine Land Cover (CLC) 2012 (Copernicus Land Monitoring Service, 2012) for circular 1km^2 areas centred on each PECBMS survey site; the habitat encompassed was taken as representative of that covered during bird surveys at that site. Open marine habitat was not the focus of this study, therefore any sites containing lagoons, estuaries, and/or sea/ocean habitats (806 in total) were removed from further analysis. In the remaining sites, habitats were aggregated into five broad types; forest, farmland, urban, wetland (including inland freshwater and coastal and inland wetlands) and semi-natural (including natural grasslands, moors, heathland, sclerophyllous vegetation and sparsely vegetated areas) (Further details in Table A.2.1.). The total areas of each of these five habitat types present at each site were calculated and sites were classified according to the dominant habitat type, *i.e.,* that which covered the largest area within each site. For each species in turn, RHU in each year t was calculated as:

$$RHU_{i,t} = \frac{n_{i,t}/p_{i,t}}{(N_t - n_{i,t})/(P_t - p_i,t)}$$

where i is the ith habitat, n_i = number of individuals in the ith habitat, p_i = number of sites of the ith habitat, N_t = total number of individuals and P_t = total number of sites surveyed in year t (Larsen *et al.,* 2011). To ensure only data from potentially available sites were included in each species' RHU calculations, P_t was calculated as the sum of all sites surveyed in year t that fell within a 50km radius buffer of sites occupied by a given species in year t.

For each species, RHU for each of the five habitat types were calculated at the European level. RHU scores can be sensitive to changes in $p_{i,t}$ especially when P_t is small, so we imposed minimum site thresholds, both across and within habitats, for a species' inclusion in subsequent analyses. RHU scores were only calculated for a given species in a given year if that species was recorded in at least 35 sites in that year, with RHU for an individual habitat only calculated if the species was recorded in at least seven sites of that habitat type in that year ($p_{i,t}$). We also specified that these site thresholds had to be met in at least three years across the 20-year period for a species to be included in our analyses. This excluded 150 species from further analyses. For the remaining 246 species, if a species was recorded in a given habitat in a given year, but at fewer than seven sites, it was assigned an "NA" RHU score for that habitat in that year. If a species was recorded in at least 35 sites in a given year but was not recorded at all in a given habitat, the species received an RHU score of zero for that habitat in that year. Very high RHU scores can potentially arise if the relative number of individuals recorded in *i*th habitat is particularly high, especially if the proportion of *i*th habitat sites is low. We therefore imposed a maximum RHU of five, with any scores above this assigned this value. Setting this maximum identified species with a very strong association with a given habitat without extremely high RHU scores skewing results. RHU scores cannot be calculated if a species is only recorded in one habitat type in a given year. In such instances, if the species was recorded in at least 35 sites of that habitat type in a given year, an RHU score of five was assigned to that species for that habitat in that year, with an RHU score of zero for all other habitats.

We recognise that classifying sites by the dominant habitat type does not necessarily capture the association of individual birds with specific patches of habitat, which may or may not be the dominant habitat type. It is therefore important to emphasise that the habitat associations reported here represent associations with landscapes dominated by a given land cover type. Habitat is a complex multidimensional concept (Kirk *et al.*, 2018), but CLC classes, based on remote sensing to determine land cover types is commonly used as a proxy for habitat (Lumbierres *et al.*, 2021). Given the spatial and temporal scale of the data used and that the average area covered by the dominant habitat type was, for forest sites: 78.4% ± 0.251%, farmland sites: 86.2% ± 0.158%, urban sites: 82.7% ± 0.384%, wetland sites: 77.9% ± 0.545% and semi-natural sites: 80.0% ± 0.419% (Fig. A.2.1.), any associations with a particular land cover type identified here infer that a substantial proportion of a species population is likely to be influenced by processes and management associated with that dominant habitat. For example, forest specialists are unlikely to be recorded in large numbers in sites dominated by habitats other than forest, relative to their counts in forest sites, so high RHU scores will only be derived for forest habitats. If, however, a species is found both in large tracts of forest and smaller forest plots or hedgerows within farmland dominated landscapes, associations with both forest and farmland habitat may be identified. Nonetheless, the farmland RHU score for such a species would still only exceed one (inferring at least a moderate association) if the proportion of total individuals found on farmland sites was greater than the proportion of total sites surveyed that were defined as farmland. Thus, a farmland RHU ≥ 1 would only be generated i) if the species is widespread across farmland sites and ii) occurs in sufficient numbers in farmland sites containing patches of suitable habitat to offset its absence from farmland sites that do not contain any suitable habitat. The species is therefore likely to also be vulnerable to management or environmental changes occurring in farmed landscapes (Boutin and Jobin, 1998; Gove *et al*., 2007).

2.3.3 Existing categorical classifications of habitat association

Categorical habitat associations for each species were extracted from a database built to support the European Environment Agency's goal to report on the state and trends of biodiversity from an ecosystem perspective, with ecosystems defined at the scale of habitat/biotope or landscape and classified by Level three CLC habitats (Maes *et al.,* 2013; Roscher *et al.,* 2015). This database reports species' associations with urban, cropland, grassland, woodland & forest, heathland & shrub, sparsely vegetated land, wetlands and rivers & lakes, with associations reported at the European scale and derived from multiple published sources; Hagemeijer and Blair (1997), Tucker and Evans (1997), Mullarney, Svensson and Zetterström (2009). From this, each species was reported as associated with a maximum of three of these habitat types. To allow direct comparison with RHU scores, we aggregated reported associations into the five over-arching habitat types outlined in section 2.3.2 and for which species' RHUs were calculated. Specifically, we combined grassland and cropland as farmland habitat, heathland & shrub and sparsely vegetated land as semi-natural and wetlands and rivers & lakes as wetland. Urban and woodland & forest (hereafter forest) remained as they were. The number of habitats each species was recorded as being associated with was used to define its degree of habitat specialisation. Hereafter, we refer to these associations as 'reported'. For example, middle-spotted woodpecker (*Leiopicus medius*) is reported as only being associated with forest, great tit (*Parus major*) is reported as being associated with both forest and urban habitats, and serin (*Serinus serinus*) is reported as being associated with forest, urban, and farmland. Whilst all three are reported as associated with forest, middle-spotted woodpecker is taken as the most specialised and serin as the most generalist of the three due to their additional habitat associations.

2.3.4 Data analysis

All calculations of RHU and statistical analyses were conducted using R version 4.0.1 (R Core Team, 2020).

2.3.4.1 RHU versus literature-based measures for habitat association

Species' RHU scores for each habitat were calculated annually using European-level data and averaged across all years to produce mean RHU scores for each habitat. We first identified all species reported in the species-habitat database (Roscher *et al.,* 2015) as being associated with only one habitat *i.e.,* most specialist species and compared their mean RHU for that habitat with their mean RHU across the other habitats for which scores were available. We then identified all species reported in the database (Roscher *et al.,* 2015) as being associated with i) two habitats and ii) three habitats and compared their mean RHU scores across those associated habitats with their mean RHU across the other habitats. Data were not normally distributed, so paired sample Wilcoxon tests were used to compare species' mean RHUs for "associated" and "not-associated" habitat(s).

Second, for species reported as associated with only one habitat we also quantified how often this habitat also had the highest mean RHU score. For species reported as being associated with two habitats, we quantified how often their mean RHUs for those habitats filled the first and second positions when ranking RHUs for all habitats, and for species reported as having three habitat associations, we quantified how often those three habitats were ranked as the top three when ranking mean RHUs for all habitats.

2.3.4.2 RHU for species' literature-based degree of habitat specialisation

For each habitat in turn, we compared the mean European-level RHUs of species reported as being i) only associated with that habitat, ii) associated with that habitat plus one other, iii) associated with that habitat plus two others, and iv) not reported as associated with that habitat. Mean RHU scores were not normally distributed so non-parametric Kruskal Wallis tests were used, with post-hoc Dunn's tests for pairwise comparisons (R package dunn.test version 1.3.5, Dinno, 2017).

2.3.4.3 Temporal variation in RHU

Using species' mean, European-level RHU across all years, we reclassified species' habitat associations according to RHU scores alone. In line with Eskildsen *et al.* (2013), species were categorized as associated with a given habitat if their mean RHU score for that habitat was ≥ 1 and not associated with the habitat if mean RHU was < 1. For those associated with a given habitat, we classified their degree of habitat specialisation according to the number of habitats for which they demonstrated a mean RHU ≥ 1. For each habitat in turn, we then explored the temporal stability of species' RHU scores according to their association with and degree of specialisation for that habitat. For each habitat, we calculated the coefficient of variation (hereafter CV) in each species' RHU over time (RHU-CV_t) as the standard deviation in its annual European-level RHU scores for that habitat, divided by its mean RHU for that habitat across years. For each habitat in turn, a GLM was then built with species' RHU-CV_t for that habitat as the dependent variable and *habitat association* (categorical term, with 'Not associated' if mean RHU < 1 and 'Associated' if mean RHU ≥ 1) as the fixed effect. For those species associated with a given habitat, a second GLM was built with species' RHU-CV_t for that habitat as the dependent variable and *degree of habitat specialisation* (categorical term, with three levels, reporting the total number of habitats with mean RHU ≥ 1 *i.e.* one, two or three-four) as the fixed effect. Only one species, *Mergus merganser* (Goosander) demonstrated mean RHU scores ≥ 1 for four habitats, so this was grouped with species with mean RHU ≥ 1 for three habitats.

2.4 Results

2.4.1 RHU-based versus literature-based measures of habitat association

Species had significantly higher RHUs for habitats they were reported as being associated with compared to RHUs for habitats they were not reported as being associated with (*One habitat: Mean RHU Associated ± SE = 2.921 ±0.12, Not associated = 0.669 ±0.03, Paired Wilcoxon test: V=5114, p < 0.001; Two habitats: Mean RHU Associated = 1.836 ±0.08, Not associated = 0.688 ±0.05, Paired Wilcoxon test: V=6148, p < 0.001; Three habitats: Mean RHU Associated = 1.548 ±0.12, Not associated = 0.498 ±0.08, Paired Wilcoxon test: V=376, p < 0.001).* The difference between mean RHUs for associated and not associated habitats decreased as the number of habitats a species was reported as being associated with increased (Fig. 2.1). Four species were excluded from this comparison because they either only had "NA" RHU scores for associated habitat(s) (three species) or for not associated habitats (one species) due to them not meeting the site thresholds (see Methods).

Of the 101 species reported as being specialised to a given habitat, the RHU for this habitat was the highest of their RHUs for any of the five habitats in 89.1% of cases. For the 113 species reported as being associated with two habitats, these habitats had the highest and second highest

RHU scores in 50.4% of cases. For the 28 species reported as being associated with three habitats, these habitats had the three highest RHU scores in 39.3% of cases. The full list of Pan-European RHU scores for each species, in each of the five over-arching habitat types are given in supplementary material, along with the literature-based association classification for each habitat type (Table A.2.2).

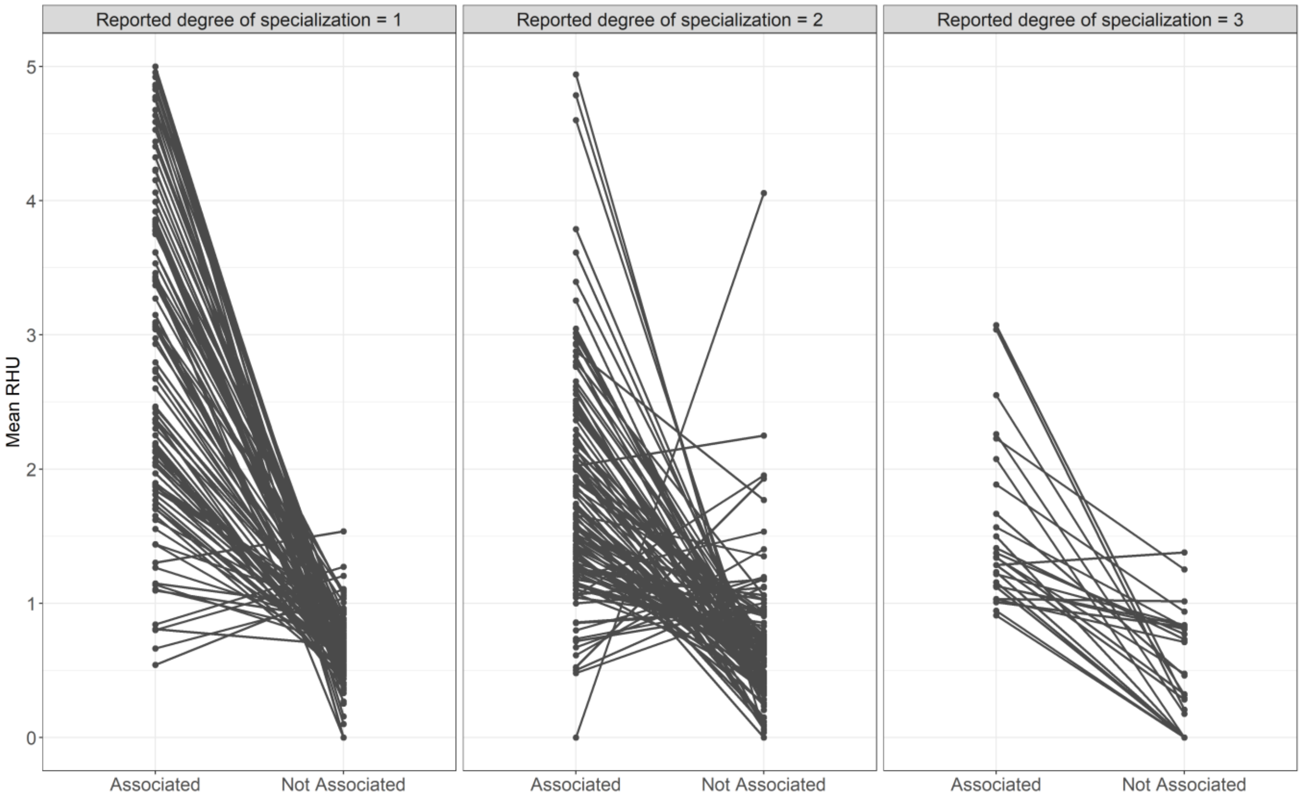


Fig. 2.1. Species' mean relative habitat use (RHU) scores for habitat(s) they were reported in the species-habitat database (Roscher *et al.*, 2015) as being associated with, versus their mean RHUs for habitats they were not reported as being associated with. Lines connect scores for individual species. Panels show results for species grouped according to their reported degree of habitat specialisation *i.e.* reported as being associated with a single habitat (Reported degree of specialisation = 1), associated with two habitats (Reported degree of specialisation = 2) or associated with three habitats (Reported degree of specialisation = 3).

2.4.2 RHU for species' literature-based degree of habitat specialisation

Species' RHUs for a given habitat were higher if they were reported as more specialised to that habitat and were always significantly higher than those for species not reported as being associated with that habitat (Fig. 2.2, Table A.2.3). Species reported as more specialised to forest habitat had significantly higher RHUs than more generalist species reported as being associated with forest (Fig. 2.2 A). Similarly, species specialised to wetland or semi-natural had significantly higher RHUs than more generalist species associated with wetland or semi-natural and one other habitat (Fig. 2.2 D, E). Species specialised to farmland had significantly higher RHUs than generalist species associated with farmland and two other habitats (Fig. 2.2 B). Furthermore, species reported as being associated with farmland or forest and one other habitat had significantly higher RHUs than more generalist species associated with either farmland or forest and two other habitats. In contrast, species associated with semi-natural habitat and one other, had significantly lower mean RHU scores than more generalist species associated with semi-natural habitat and two others (Table A.2.3.).

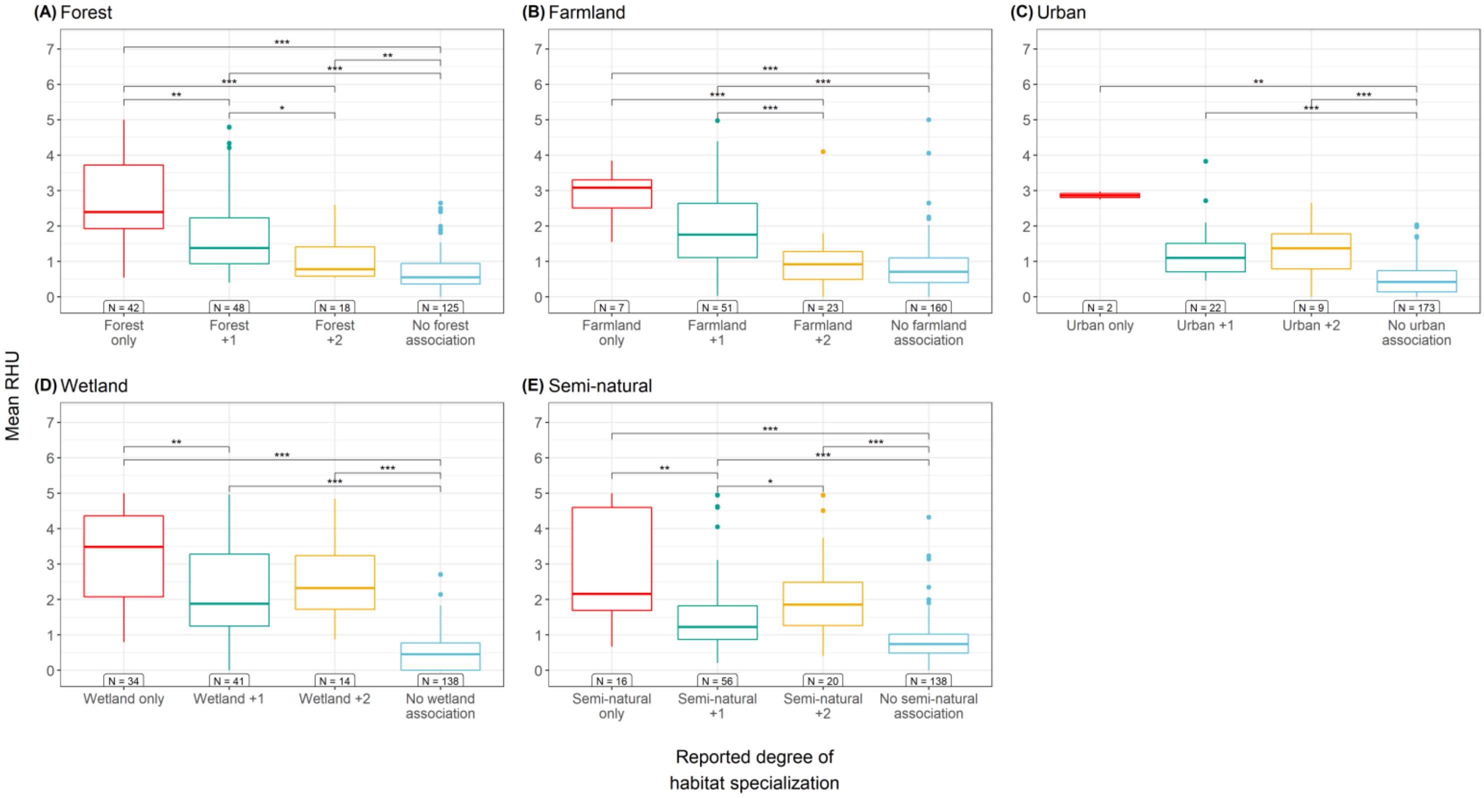


Fig. 2.2. Species mean relative habitat use (RHU) scores for A) forest., B) farmland, C) urban, D) wetland and E) semi-natural habitats. Within the panel for each habitat, species are grouped according to their reported degree of habitat specialisation, determined by the number of habitats they have been reported as being associated with or if not reported as being associated with the panel habitat (Roscher *et al.*, 2015). Sample size for each group is given under each boxplot. Pairwise comparisons showing significant differences are also identified (* p<0.05, ** p<0.01, *** p<0.001).

2.4.3 Temporal variation in RHU

RHU-CV_t for species associated with farmland or urban habitats were significantly lower than species not associated with these habitats, but it did not vary significantly according to degree of specialisation (Table 2.1). RHU-CV_t for species associated with forest habitats was significantly lower than for species not associated with forests and also declined as degree of specialisation for forest increased (Table 2.1, Fig. 2.3 A). For wetland and semi-natural habitats, there was no significant difference in RHU-CV_t between associated and not associated species, but more generalist species with a degree of specialisation of two and three – four habitats respectively had significantly higher RHU-CV_t scores than those more specialised to wetland or semi-natural (Table 2.1, Fig. 2.3 D, E).

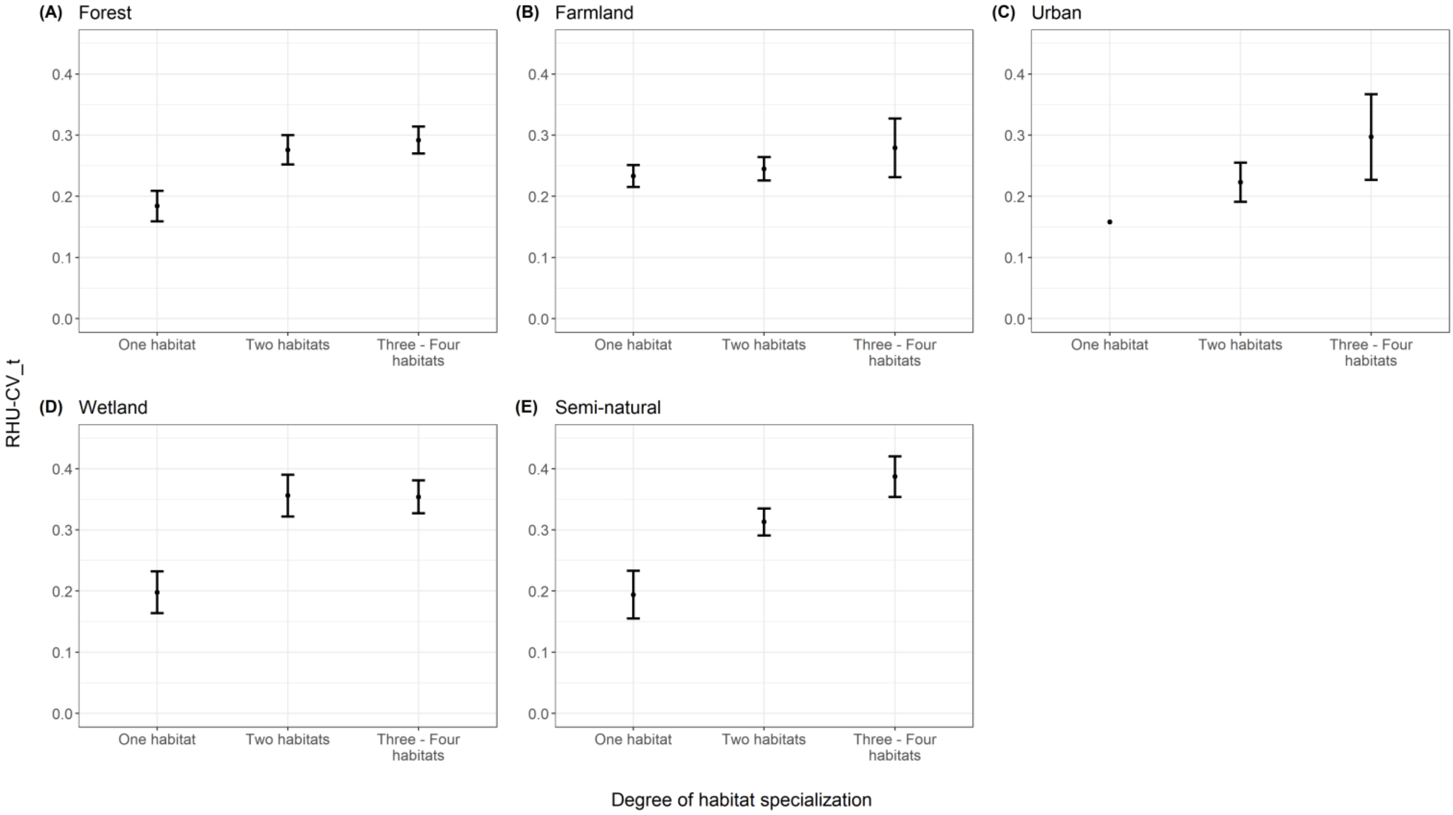


Fig. 2.3. Mean coefficient of variation in relative habitat use over time (RHU-CV_t (± SE)) for species associated with A) forest, B) farmland, C) urban, D) wetland and E) semi-natural habitats, according to their degree of habitat specialisation, defined as the total number of habitats for which they had a mean RHU ≥ 1.

Table 2.1. Estimated model parameters, standard errors, t-values and p-values from GLMs examining the influence of habitat association and degree of habitat specialisation on RHU-CV_t. Separate models were run with i) species' association with that specific habitat, defined by mean RHU score for that habitat (Not associated = mean RHU < 1, Associated = mean RHU ≥ 1) and ii) for those species associated with a given habitat, their degree of specialisation, defined as the total number of habitats for which they had a mean RHU ≥ 1, as fixed effects. Significant terms are highlighted in bold.

Habitat	*Predictor*	*Term*	*Estimate*	*std. error*	*t -statistic*	*p-value*
Forest	Association	Intercept	0.310	0.015	21.223	**<0.001**
		Associated	-0.050	0.021	-2.356	**0.019**
	Degree of habitat specialisation	Intercept	0.184	0.029	6.305	**<0.001**
		Two habitats	0.092	0.036	2.561	**0.012**
		Three – Four habitats	0.108	0.038	2.807	**0.006**
Farmland	Association	Intercept	0.352	0.019	18.389	**<0.001**
		Associated	-0.104	0.029	-3.607	**<0.001**
	Degree of habitat specialisation	Intercept	0.233	0.026	8.900	**<0.001**
		Two habitats	0.012	0.034	0.350	0.727
		Three – Four habitats	0.046	0.041	1.124	0.264
Urban	Association	Intercept	0.363	0.025	14.629	**<0.001**
		Associated	-0.119	0.048	-2.460	**0.015**
	Degree of habitat specialisation	Intercept	0.158	0.197	0.800	0.428
		Two habitats	0.065	0.201	0.324	0.748
		Three – Four habitats	0.139	0.205	0.677	0.502
Wetland	Association	Intercept	0.369	0.028	13.012	**<0.001**
		Associated	-0.027	0.039	-0.690	0.491

	Degree of habitat specialisation	Intercept	0.198	0.072	2.748	**0.007**
		Two habitats	0.158	0.078	2.033	**0.045**
		Three – Four habitats	0.156	0.079	1.966	0.052
Semi-natural	Association	Intercept	0.317	0.017	19.110	**<0.001**
		Associated	0.011	0.024	0.458	0.647
	Degree of habitat specialisation	Intercept	0.194	0.060	3.255	**0.002**
		Two habitats	0.120	0.064	1.872	0.064
		Three – Four habitats	0.193	0.067	2.901	**0.005**

2.5 Discussion

We show that RHU and literature-derived classifications for habitat association and degree of specialisation are generally well aligned, although there are some disparities. Overall, species demonstrate higher RHU scores for habitat(s) they are reported as being associated with in the literature. Similarly, species reported as being associated with a given habitat have higher RHUs for that habitat compared to species not reported as being associated with it. RHU also differentiates species according to their degree of habitat specialisation, with species more specialised to a given habitat having higher mean RHU scores for that habitat than more generalist species that are associated with it. Finally, we show that within the temporal scale of this study, species associated with a given habitat show lower variation in RHU scores for that habitat over time compared to species not associated with it. Furthermore, species more specialised to a given habitat show less variation in their RHUs for that habitat over time compared to more generalist species.

We expect literature-based classifications and RHU to align with one another as both methods rely on observations of species' abundances across habitats to characterise their habitat associations. However, we do identify some instances where RHU and literature-based classifications differ, which are likely to be driven by data collection methods and habitat classification, as well as the specific ecology of individual species. For example, we find that 29 out of 34 species reported as being specialised to wetland habitats also have mean RHUs $\geq$ 1 for at least one terrestrial habitat (i.e. forest, farmland, semi-natural and urban). Furthermore, for five of these 29 species, their RHUs for at least one terrestrial habitat is greater than their RHUs for wetland habitat. This suggests that these "wetland" species are counted in higher numbers in terrestrial habitats than is expected given relative habitat availability. It is important to note that the number of wetland dominated sites surveyed is considerably lower than the number of terrestrial dominated sites surveyed (Table A.2.4). This is due to the fact that the national monitoring schemes are targeted towards terrestrial habitats and therefore more terrestrial species. In addition to this, these "wetland" species may also be counted on patches of wetland habitat within sites dominated by a terrestrial habitat. In this study, RHU calculates species' association with landscapes dominated by a given habitat. In contrast, literature-based classifications for species' habitat associations are derived from observations of species' use of particular habitat types. It is therefore likely that these wetland species are counted in higher numbers on wetland patches within terrestrial dominated sites compared to the number of individuals counted on wetland dominated sites. Furthermore, if the number of wetland dominated sites are under-represented due to the underlying data collection methods mentioned, than there are not enough wetland sites available, with wetland species counts to offset the number of terrestrial dominated sites which these wetland species are counted in. As a result, RHU scores for terrestrial habitat will be higher than wetland habitat RHU scores. Therefore, the habitat classification approach adopted in this study means that RHU can be limited if species' use of small patches of preferred habitat within a landscape matrix is important. Count data from surveys targeted towards wetlands such as the UK Waterways Breeding Bird Survey (Harris *et al*., 2019), Waterfowl Monitoring in Lakes in Finland (Laaksonen *et al*., 2019) and Spring Waterbirds Census in Belgium (Weiserbs, 2012) could be integrated to provide additional count data for wetland species on wetland dominated sites. Doing so would mean that wetland dominated sites would have higher species' counts relative to the species' counts in terrestrial dominated sites that contain patches of wetland habitat. A unit increase in the number of wetland sites increases the counts for wetland species. This in turn would offset species' counts in terrestrial dominated sites that contain wetland patches, thereby resulting in higher RHU scores for wetland habitat and lower scores for terrestrial habitats.

We also find that 21 out of 149 species reported as only associated with terrestrial habitats have mean RHUs ≥ 1 for wetland habitat, with nine of these having higher mean RHUs for wetland habitat compared to their mean RHUs for some of their associated terrestrial habitats. This further suggests that species' habitat use at a finer spatial scale has an impact on how well RHU and literature-based classification reflect one another. Our definition of wetland habitat in this study includes inland wetlands such as marshes and peat bogs. Although these habitat types are characteristically water-logged areas, they also contain vegetation in the form of herbaceous or woody plants, dwarf shrubs, sedges, willows, mosses or scattered trees, which are also found in terrestrial habitats (Copernicus Land Monitoring Service., 2012). Therefore, it is unsurprising that some species reported as only being associated with terrestrial habitats may have mean RHUs ≥ 1 for wetlands, if they are counted in wetland sites that contain similar vegetation to terrestrial habitats. Similarly, the Roscher *et al*. (2015) database used in this study does not report that *Himantopus himantopus* (Black-winged stilt) is associated with farmland but analyses of relative abundance across habitats from PECBMS data identifies a mean RHU of 4.058 for farmland. Similarly, *Luscinia luscinia* (Thrush nightingale) is not reported as associated with urban habitat, yet has an RHU of 1.579 for it. This further suggests that the approach used in this study to classify sites by the dominant habitat type means that RHU and literature-derived classifications are less likely to reflect one another. In particular when species' specific ecology is important, as is the case with these two species for example. Other literature sources reporting on specific habitat use of these species suggest that Black-winged stilt is found on irrigated farmland or wet pastures (BirdLife International, 2021), and Thrush nightingale can be found in urban parks and gardens (Csörgő *et al*., 2018). Classifying sites by the dominant habitat means that species' association with and degree of specialisation for habitats is interpreted in a wider landscape context. This highlights a weakness in RHU in that it identifies associations with habitats that it is not necessarily associated with.

Interestingly, the pattern of difference in mean RHUs between species grouped by their reported degree of specialisation for semi-natural habitat deviate from those for the other habitats. One explanation for this is that semi-natural habitat encompasses a range of CLC Level three habitats (see Table A.2.1), where there is greater variation within this habitat type compared to the variation within the other four habitats. Therefore, our interpretation of results for semi-natural should be treated with caution, as species' association with some habitats grouped under semi-natural are stronger than their associations with other habitats grouped under semi-natural, thereby producing results that do not follow the same pattern as other habitats. We recommend that exploration of the RHU metric for this varied habitat type should consider calculating species' RHUs for each CLC Level three habitat separately.

Variation in detectability could also introduce bias to species' RHU scores. In such cases, reduced detectability in closed habitats (Johnston *et al*., 2014) such as forest and urban could lead to lower counts in, and thus lower RHU scores for, those habitats. In turn, this would under-estimate the extent of their associations with closed habitats and over-estimate their associations with more open habitats (*e.g.*, farmland and semi-natural) (Larsen *et al*., 2011). This issue is most likely to arise for generalist species that are relatively evenly distributed across a range of habitats. However, the potential influence of varying detectability on the assessment of a species' association and specialisation will decrease as that species' specialisation increases. Even if a species is specialised to a closed habitat, the variation in RHU scores between habitats will become more pronounced as counts become increasingly skewed towards the closed habitat. Detectability is therefore less likely to impact specialist species, which is an important factor to consider if the RHU approach is used to identify habitat specialists that will in turn advise conservation management.

There are also limitations that come with relying on the categorical, literature-based approach. For example, static, categorical classifications which are based on small-scale field studies, observations or expert-opinion simply group species into those that are associated or not associated with a habitat and whether those associated are specialists or generalists. This fails to account for variation between species in the extent of their association with or specialisation for a habitat. Although there are specific limitations with RHU, overall it is more robust than categorical-based classifications as it is a quantitative method that is based on the most widely available data, can be calculated at any temporal or spatial scale, and can differentiate species based on the extent of their association with or degree of specialisation for a given habitat. Within the time frame of this study, species associated with and more specialised to a given habitat do not show large temporal variation in their RHU scores for that habitat over time. Furthermore, species that are less specialised to a habitat have higher temporal variation in RHU scores due to their capacity to exploit different habitat types for required resources. By comparison, more specialised species are limited in the number of habitats they are capable of using, as the environmental conditions and resources they require for foraging or breeding will be found in a single or limited number of habitats. These results give us further confidence in using RHU to classify species as associated with or more specialised to a given habitat as these species are unlikely to vary in their habitat associations over time.

2.6 Conclusion

We find that quantitative, RHU-based assessments of species' association with and degree of specialisation for a given habitat are broadly similar to literature-based categorical classifications. We also find that RHU scores for given habitat are relatively stable in time, particularly if associated with and more specialised to that habitat. While there is general consistency between these two methods, RHU offers a more robust approach by quantifying the extent of species' association with each habitat in which it is recorded. Calculating RHU scores annually allows classifications for association and specialisation to also be updated if necessary. We therefore recommend that the RHU metric should be considered further as a useful tool to identify and classify species by their habitat associations and degree of specialisation. Doing so would support conservation management strategies to protect habitat specialists and their habitats, and thus support national and international progress towards reaching biodiversity targets.

2.7 Appendices

Table A.2.1. Corine Land Cover 2012 Levels 1 – 3 with habitat category assigned to each Level 3 habitat

Assigned habitat category	Level 1	Level 2	Level 3
Urban	Artificial surfaces	Urban fabric	Continuous urban fabric
			Discontinuous urban fabric
		Industrial, commercial and transport units	Industrial or commercial units
			Road and rail networks and associated land
			Port areas
			Airports
		Mine, dump and construction sites	Mineral extraction sites
			Dump sites
			Construction sites
		Artificial, non-agricultural vegetated areas	Green urban areas
			Sport and leisure facilities
Farmland	Agricultural areas	Arable land	Non-irrigated arable land

		Permanent crops	Permanently irrigated land
			Rice fields
			Vineyards
			Fruit trees and berry plantations
			Olive groves
		Pastures	Pastures
		Heterogeneous agricultural areas	Annual crops associated with permanent crops
			Complex cultivation patterns
			Land principally occupied by agriculture, with significant areas of natural vegetation
			Agro-forestry areas
Forest	Forest and semi natural areas	Forests	Broad-leaved forest
			Coniferous forest
			Mixed forest
Semi-natural	Forest and semi natural areas	Scrub and/or herbaceous vegetation associations	Natural grasslands
			Moors and heathland
			Sclerophyllous vegetation

			Transitional woodland-shrub
		Open spaces with little or no vegetation	Beaches, dunes, sands
			Bare rocks
			Sparsely vegetated areas
			Burnt areas
			Glaciers and perpetual snow
Wetland	Wetlands	Inland wetlands	Inland marshes
			Peat bogs
		Maritime wetlands	Salt marshes
			Salines
			Intertidal flats
	Water bodies	Inland waters	Water courses
			Water bodies

Table A.2.2. Pan-European mean RHU scores for each species (246 total), for each of the five over-arching habitat types, with literature-based habitat association classifications for each habitat..

		Pan-European mean RHU					**Literature-based habitat association classification**				
EURING	Species	Forest	Farmland	Urban	Aquatic	Semi-natural	Forest	Farmland	Urban	Aquatic	Semi-natural
20	*Gavia stellata*	1.146	NA	0	1.265	1.315	0	0	0	1	0
30	*Gavia arctica*	1.086	0.355	0	1.767	0.86	0	0	0	1	0
70	*Tachybaptus ruficollis*	0.939	0.783	0.775	3.615	0.843	0	0	0	1	0
90	*Podiceps cristatus*	0.962	0.526	1.207	4.678	0.5	0	0	0	1	0
100	*Podiceps grisegena*	1.043	1.253	1.46	NA	0	0	0	0	1	0
720	*Phalacrocorax carbo*	0.849	0.585	0.502	4.154	0.753	0	0	0	1	0
950	*Botaurus stellaris*	0.893	0.728	0.772	3.993	0.576	0	0	0	1	0
1110	*Bubulcus ibis*	0.174	3.637	1.615	0	0.316	0	1	0	1	0
1190	*Egretta garzetta*	0.317	1.668	0.637	3.271	0.408	0	0	0	1	0
1210	*Egretta alba*	NA	5	NA	NA	NA	0	0	0	1	1
1220	*Ardea cinerea*	0.719	1.288	1.114	1.878	0.313	1	0	0	1	0
1310	*Ciconia nigra*	1.005	1.124	NA	0	NA	1	0	0	1	0
1340	*Ciconia ciconia*	0.413	2.06	0.461	1.662	1.01	0	1	1	0	0
1520	*Cygnus olor*	0.565	1.183	1.346	1.896	0.252	0	0	0	1	0
1540	*Cygnus cygnus*	1.994	0.488	0	1.512	1.356	0	1	0	1	0
1610	*Anser anser*	0.785	0.818	0.861	2.581	1.298	0	1	0	1	1
1660	*Branta canadensis*	0.636	0.971	1.575	1.942	0.539	0	0	0	1	1
1670	*Branta leucopsis*	NA	0.44	1.782	2.961	NA	0	1	1	1	1
1730	*Tadorna tadorna*	0.341	0.952	0.419	3.29	1.521	0	0	0	1	1
1790	*Anas penelope*	1.535	0.501	NA	3.435	1.23	0	0	0	1	0
1820	*Anas strepera*	0.514	0.791	0.557	4.443	1.013	0	0	0	1	0
1840	*Anas crecca*	1.029	0.315	0.454	4.922	0.854	0	0	0	1	0
1860	*Anas platyrhynchos*	0.442	1.228	1.679	1.841	0.412	0	0	0	1	0
1910	*Anas querquedula*	0.45	1.192	NA	3.533	0.671	0	0	0	1	0
1940	*Anas clypeata*	0.347	0.461	0.23	4.529	1.426	0	0	0	1	0
1980	*Aythya ferina*	1.006	0.819	0.644	3.921	0.708	0	0	0	1	0
2030	*Aythya fuligula*	0.895	0.778	1.064	3.127	0.576	0	0	0	1	1
2180	*Bucephala clangula*	2.307	0.499	0.757	1.8	0.688	1	0	0	1	0
2210	*Mergus serrator*	1.11	0.772	NA	2.081	1.762	0	0	0	1	1
2230	*Mergus merganser*	2.416	0.475	1.706	1.274	1.124	0	0	0	1	1
2310	*Pernis apivorus*	1.873	1.062	NA	0	1.086	1	0	0	0	0
2380	*Milvus migrans*	0.461	2.207	0.433	1.671	0.896	1	0	0	1	0

2390	*Milvus milvus*	0.995	1.619	0.424	0.473	0.962	1	0	0	1	0
2430	*Haliaeetus albicilla*	1.056	0.766	NA	NA	3.142	1	0	0	1	0
2470	*Neophron percnopterus*	0.641	1.205	0	0	1.651	0	0	0	0	1
2510	*Gyps fulvus*	1.216	0.631	0.113	0	1.706	0	0	0	0	1
2560	*Circaetus gallicus*	0.637	1.39	0	0	1.338	1	1	0	0	1
2600	*Circus aeruginosus*	0.307	1.731	0.344	2.796	1.001	0	0	0	1	0
2610	*Circus cyaneus*	0.925	0.922	0	1.733	2.348	0	1	0	1	1
2630	*Circus pygargus*	0.233	3.077	NA	0	0.92	0	1	0	0	1
2670	*Accipiter gentilis*	2.454	0.567	0.431	1.414	0.99	1	0	0	0	0
2690	*Accipiter nisus*	1.148	1.161	1.06	0.56	0.573	1	0	1	0	0
2870	*Buteo buteo*	1.027	1.634	0.374	0.5	0.726	1	1	0	0	0
2900	*Buteo lagopus*	0.922	0	0	NA	1.809	1	1	0	0	1
2960	*Aquila chrysaetos*	0.947	0.46	0	NA	2.174	0	0	0	0	1
2980	*Hieraaetus pennatus*	1.086	1.024	0.575	0	1.055	1	0	0	0	1
3010	*Pandion haliaetus*	2.403	0.467	0	3.28	NA	1	0	0	1	0
3030	*Falco naumanni*	NA	4.098	0	0	0.403	0	1	1	0	1
3040	*Falco tinnunculus*	0.483	1.969	0.716	0.529	0.854	0	1	0	0	0
3090	*Falco columbarius*	2.595	0.323	0	3.331	2.055	1	1	0	1	1
3100	*Falco subbuteo*	1.413	1.108	0.518	1.714	0.944	1	1	0	1	0
3200	*Falco peregrinus*	1.35	0.527	0.754	2.015	2.887	0	0	1	1	1
3260	*Bonasa bonasia*	2.193	0.34	0	1.03	0.754	1	0	0	0	0
3290	*Lagopus lagopus*	0.604	0	0	1.192	1.899	1	0	0	1	1
3320	*Tetrao tetrix*	3.046	0.199	NA	1.118	0.832	1	0	0	0	1
3350	*Tetrao urogallus*	2.253	NA	0	0.821	0.739	1	0	0	0	0
3580	*Alectoris rufa*	0.491	2.591	0.239	0.224	0.893	0	1	0	0	1
3670	*Perdix perdix*	0.198	4.392	0.353	0.409	0.334	0	1	0	0	1
3700	*Coturnix coturnix*	0.465	3.15	0.146	0.343	0.899	0	1	0	0	0
4070	*Rallus aquaticus*	0.474	0.438	0.429	4.831	1.228	0	0	0	1	0
4210	*Crex crex*	1.175	1.559	0.381	NA	1.188	0	1	0	1	0
4240	*Gallinula chloropus*	0.389	1.174	1.976	1.147	0.313	0	0	0	1	0
4290	*Fulica atra*	0.664	0.881	1.496	2.934	0.376	0	0	0	1	0
4330	*Grus grus*	1.013	1.528	0.134	1.345	0.544	0	1	0	1	0
4420	*Tetrax tetrax*	NA	3.843	NA	0	0.713	0	1	0	0	0
4460	*Otis tarda*	NA	3.461	NA	0	NA	0	1	0	0	0
4500	*Haematopus ostralegus*	0.22	0.619	0.55	4.035	1.994	0	0	0	1	1
4550	*Himantopus himantopus*	NA	4.058	NA	0	NA	0	0	0	1	1
4560	*Recurvirostra avosetta*	0	0.932	NA	4.751	0.371	0	0	0	1	1
4590	*Burhinus oedicnemus*	0.176	3.409	NA	0	1.085	0	1	0	0	1
4690	*Charadrius dubius*	0.565	1.009	0.609	3.296	0.983	0	0	0	1	1

4700	*Charadrius hiaticula*	0.312	0.601	NA	3.581	2.295	0	0	0	1	1
4850	*Pluvialis apricaria*	0.35	0.225	0	2.052	4.506	0	1	0	1	1
4930	*Vanellus vanellus*	0.271	2.005	0.269	2.425	0.899	0	1	0	1	0
5120	*Calidris alpina*	0	1.394	0	3.186	1.691	0	0	0	1	1
5190	*Gallinago gallinago*	1.905	0.366	0.144	3.094	1.902	0	0	0	1	0
5290	*Scolopax rusticola*	4.324	0.332	NA	0.918	1.022	1	0	0	0	0
5320	*Limosa limosa*	0	3.516	0.282	1.506	0.483	0	1	0	1	0
5380	*Numenius phaeopus*	2.244	0.207	NA	3.519	3.357	1	0	0	1	1
5410	*Numenius arquata*	0.683	0.657	0.142	2.659	3.228	0	1	0	1	0
5460	*Tringa totanus*	0.436	0.549	0.198	4.846	2.261	0	1	0	1	1
5480	*Tringa nebularia*	2.646	0.107	0	2.35	1.46	0	0	0	1	1
5530	*Tringa ochropus*	4.336	0.251	0.196	1.213	0.944	1	0	0	1	0
5540	*Tringa glareola*	1.162	0.172	0	2.601	1.497	0	0	0	1	0
5560	*Actitis hypoleucos*	2.405	0.249	0.522	3.855	1.747	0	0	0	1	1
5680	*Stercorarius longicaudus*	NA	0	0	NA	4.773	0	0	0	0	1
5820	*Larus ridibundus*	0.311	0.732	0.905	4.511	0.722	0	0	0	1	1
5900	*Larus canus*	0.98	0.651	0.738	1.575	2.435	0	0	0	1	1
5910	*Larus fuscus*	0.156	0.308	0.937	3.526	4.051	0	0	0	1	1
5920	*Larus argentatus*	0.321	0.537	1.276	3.221	2.633	0	0	0	1	1
6150	*Sterna hirundo*	0.418	0.358	0.308	4.965	1.128	0	0	0	1	1
6160	*Sterna paradisaea*	0.483	0.719	0	3.912	1.026	0	0	0	1	1
6650	*Columba livia*	0.194	1.315	3.831	0.757	0.55	0	0	1	0	1
6680	*Columba oenas*	0.832	1.753	0.653	0.572	0.521	1	1	0	0	0
6700	*Columba palumbus*	0.578	1.799	1.478	0.32	0.243	1	1	1	0	0
6840	*Streptopelia decaocto*	0.325	1.257	2.975	0.213	0.156	0	0	1	0	0
6870	*Streptopelia turtur*	1.327	1.364	0.241	0.392	1.036	1	1	0	0	0
7160	*Clamator glandarius*	0.498	2.257	0	0	0.806	0	0	0	0	1
7240	*Cuculus canorus*	2.101	0.667	0.39	0.887	1.283	1	1	0	1	0
7350	*Tyto alba*	NA	2.878	NA	1.77	NA	0	1	1	0	0
7570	*Athene noctua*	0.549	2.612	0.297	NA	0.999	1	1	0	0	0
7610	*Strix aluco*	2.674	0.882	0.476	0.622	0.748	1	0	0	0	0
7670	*Asio otus*	2.104	0.852	1.061	1.065	0.963	1	1	0	0	0
7680	*Asio flammeus*	2.504	0.265	0	2.68	3.74	0	1	0	1	1
7780	*Caprimulgus europaeus*	4.787	0.411	0	NA	NA	1	0	0	0	1
7950	*Apus apus*	0.625	0.83	2.658	0.71	0.84	1	0	1	0	1
8310	*Alcedo atthis*	1.306	1.105	0.902	1.439	0.52	0	0	0	1	0
8400	*Merops apiaster*	0.519	2.016	0.381	0	0.959	0	0	0	1	1
8460	*Upupa epops*	0.588	1.554	0.417	0.195	1.465	0	1	0	0	0

8480	*Jynx torquilla*	1.159	1.039	0.66	0.819	1.014	1	1	0	0	0
8550	*Picus canus*	1.621	0.701	0.701	1.054	0.927	1	0	0	0	0
8560	*Picus viridis*	1.275	1.176	0.87	0.267	0.625	1	1	0	0	0
8630	*Dryocopus martius*	3.776	0.405	0.267	0.531	0.674	1	0	0	0	0
8760	*Dendrocopos major*	2.568	0.661	0.789	0.495	0.457	1	1	1	0	0
8830	*Dendrocopos medius*	3.782	0.388	0.533	NA	NA	1	0	0	0	0
8870	*Dendrocopos minor*	2.466	0.746	0.531	0.962	0.79	1	0	0	0	0
8980	*Dendrocopos tridactylus*	2.37	NA	0	NA	0.785	1	0	0	0	0
9610	*Melanocorypha calandra*	0.169	4.976	NA	0	0.205	0	1	0	0	1
9680	*Calandrella brachydactyla*	0.119	3.845	NA	0	0.449	0	1	0	0	1
9720	*Galerida cristata*	0.256	3.517	0.558	NA	0.662	0	1	1	0	0
9730	*Galerida theklae*	0.278	1.689	0	0	1.603	0	1	0	0	1
9740	*Lullula arborea*	1.774	0.698	0.141	NA	2.812	1	0	0	0	1
9760	*Alauda arvensis*	0.331	3.042	0.314	0.64	0.763	0	1	0	0	0
9810	*Riparia riparia*	0.697	1.66	0.757	1.597	0.464	0	0	1	1	0
9910	*Ptyonoprogne rupestris*	1.258	0.475	NA	0	2.347	0	0	0	0	1
9920	*Hirundo rustica*	0.431	2.679	0.577	0.561	0.473	0	1	1	0	0
9950	*Hirundo daurica*	0.92	1.271	NA	0	1.149	0	0	1	0	1
10010	*Delichon urbicum*	0.553	1.686	1.148	0.578	0.556	0	0	1	0	1
10050	*Anthus campestris*	0.45	1.277	0	0	2.323	0	1	0	0	1
10090	*Anthus trivialis*	4.798	0.25	0.123	1.331	1.165	1	0	0	0	1
10110	*Anthus pratensis*	0.468	0.323	0.114	3.948	4.946	0	1	0	1	1
10140	*Anthus spinoletta*	0.664	0.291	0	NA	4.602	0	0	0	1	1
10170	*Motacilla flava*	0.855	1.755	0.114	1.671	0.742	0	1	0	1	0
10190	*Motacilla cinerea*	1.393	0.663	1.06	0.8	1.702	0	0	0	1	0
10200	*Motacilla alba*	0.807	1.458	0.917	0.797	0.584	0	0	1	1	0
10480	*Bombycilla garrulus*	1.884	0.068	0	1.017	1.19	1	0	0	0	0
10500	*Cinclus cinclus*	1.813	0.544	0.909	0.841	1.819	0	0	0	1	0
10660	*Troglodytes troglodytes*	1.096	1.095	1.09	0.63	0.689	1	0	0	0	0
10840	*Prunella modularis*	0.852	1.157	1.303	0.49	0.866	1	0	1	0	1
10940	*Prunella collaris*	0.468	NA	0	0	4.755	0	0	0	0	1
10990	*Erithacus rubecula*	1.828	0.806	1.011	0.461	0.621	1	0	1	0	0
11030	*Luscinia luscinia*	0.402	1.872	1.579	0.825	0.755	1	0	0	1	0
11040	*Luscinia megarhynchos*	0.968	1.315	0.473	0.375	1.742	1	0	0	1	0
11060	*Luscinia svecica*	0.751	0.42	0.296	3.259	1.721	0	0	0	1	1
11210	*Phoenicurus ochruros*	0.759	1.114	1.521	0.35	1.285	0	0	1	0	1
11220	*Phoenicurus phoenicurus*	3.409	0.31	0.536	1.402	1.256	1	0	0	0	0

11370	*Saxicola rubetra*	1.414	0.972	0.198	0.868	1.545	0	1	0	1	1
11390	*Saxicola torquatus*	1.02	0.974	0.27	0.97	2.06	0	1	0	0	1
11460	*Oenanthe oenanthe*	0.596	0.353	0.174	1.242	4.954	0	1	0	0	1
11480	*Oenanthe hispanica*	0.647	1.417	NA	0	1.139	0	0	0	0	1
11660	*Monticola solitarius*	0.642	0.544	NA	0	3.779	0	0	0	0	1
11860	*Turdus torquatus*	1.887	0.18	0	0.672	4.625	1	0	0	0	1
11870	*Turdus merula*	0.937	1.095	1.842	0.41	0.391	1	0	1	0	0
11980	*Turdus pilaris*	1.871	0.713	0.743	1.365	0.694	1	0	0	0	0
12000	*Turdus philomelos*	2.127	0.793	0.74	0.528	0.549	1	0	0	0	0
12010	*Turdus iliacus*	3.753	0.234	0.307	1.831	1.172	1	0	0	0	0
12020	*Turdus viscivorus*	1.852	0.789	0.652	0.455	1.118	1	0	0	0	1
12200	*Cettia cetti*	0.912	1.033	0.77	3.06	1.311	0	0	0	1	0
12260	*Cisticola juncidis*	0.321	3.082	0.999	0.773	0.3	0	1	0	0	0
12360	*Locustella naevia*	0.821	0.594	0.463	3.776	2.349	0	0	0	1	0
12370	*Locustella fluviatilis*	0.94	1.163	0.808	NA	NA	0	0	0	1	0
12380	*Locustella luscinioides*	0.226	0.438	NA	4.957	NA	0	0	0	1	0
12430	*Acrocephalus schoenobaenus*	0.458	0.885	0.522	4.232	0.824	0	0	0	1	0
12480	*Acrocephalus dumetorum*	0.524	1.821	2.037	NA	NA	1	0	0	1	0
12500	*Acrocephalus palustris*	0.363	2.024	0.738	1.89	0.66	0	0	0	1	0
12510	*Acrocephalus scirpaceus*	0.437	0.732	0.716	4.865	0.697	0	0	0	1	0
12530	*Acrocephalus arundinaceus*	0.563	1.607	0.718	2.727	0.29	0	0	0	1	0
12590	*Hippolais icterina*	0.54	1.713	1.101	0.917	0.687	1	0	0	0	0
12600	*Hippolais polyglotta*	0.649	1.75	0.547	0.548	0.785	1	0	0	0	1
12620	*Sylvia undata*	1.144	0.295	NA	0	4.636	0	0	0	0	1
12640	*Sylvia conspicillata*	NA	0.874	0	0	2.322	0	1	0	0	1
12650	*Sylvia cantillans*	1.19	0.61	NA	0	2.027	0	0	0	0	1
12670	*Sylvia melanocephala*	0.873	0.766	1.227	0	1.614	1	0	0	0	1
12720	*Sylvia hortensis*	0.715	1.077	0	0	1.68	1	1	0	0	1
12730	*Sylvia nisoria*	0.543	1.346	NA	0	NA	1	1	0	0	1
12740	*Sylvia curruca*	1.405	0.83	0.926	0.742	1.147	1	1	0	0	1
12750	*Sylvia communis*	0.528	1.917	0.7	0.969	0.605	0	1	0	0	1
12760	*Sylvia borin*	2.303	0.634	0.641	1.451	0.606	1	0	0	0	0
12770	*Sylvia atricapilla*	1.81	0.897	0.959	0.536	0.397	1	0	0	0	0
12930	*Phylloscopus trochiloides*	2.126	0.406	NA	NA	NA	1	0	0	0	0
13070	*Phylloscopus bonelli*	1.732	0.583	0.199	0	1.484	1	0	0	0	0
13080	*Phylloscopus sibilatrix*	4.855	0.313	0.413	0.555	0.475	1	0	0	0	0
13110	*Phylloscopus collybita*	1.649	0.925	0.981	0.659	0.437	1	0	0	0	1

13120	*Phylloscopus trochilus*	4.156	0.277	0.324	1.555	1.37	1	0	0	0	1
13140	*Regulus regulus*	3.861	0.431	0.42	0.572	0.932	1	0	0	0	0
13150	*Regulus ignicapillus*	3.422	0.492	0.389	0.445	1.003	1	0	0	0	0
13350	*Muscicapa striata*	3.681	0.463	0.498	0.976	0.653	1	0	1	0	0
13430	*Ficedula parva*	3.403	0.268	NA	NA	NA	1	0	0	0	0
13480	*Ficedula albicollis*	1.625	0.772	1.138	0	0	1	0	1	0	0
13490	*Ficedula hypoleuca*	4.21	0.336	0.692	0.933	0.404	1	0	1	0	0
13640	*Panurus biarmicus*	NA	0.252	NA	5	NA	0	0	0	1	0
14370	*Aegithalos caudatus*	1.433	0.972	1.156	0.446	0.601	1	1	0	0	0
14400	*Poecile palustris*	3.825	0.538	0.549	0.488	0.393	1	0	0	0	0
14420	*Poecile montanus*	4.062	0.241	0.194	1.257	1.989	1	0	0	0	0
14540	*Lophophanes cristatus*	3.809	0.279	0.302	0.305	1.519	1	0	0	0	0
14610	*Periparus ater*	3.617	0.41	0.432	0.36	1.464	1	0	0	0	0
14620	*Cyanistes caeruleus*	0.904	1.188	1.761	0.37	0.309	1	0	1	0	0
14640	*Parus major*	1.478	0.892	1.459	0.442	0.4	1	0	1	0	0
14790	*Sitta europaea*	3.066	0.593	0.867	0.368	0.347	1	0	0	0	0
14860	*Certhia familiaris*	3.369	0.437	0.378	0.519	1.481	1	0	0	0	0
14870	*Certhia brachydactyla*	2.049	0.74	0.978	0.454	0.622	1	0	0	0	0
14900	*Remiz pendulinus*	NA	1.021	1.261	4.223	0	0	0	0	1	0
15080	*Oriolus oriolus*	1.104	1.45	0.493	0.36	0.737	1	0	0	0	0
15150	*Lanius collurio*	0.838	1.545	0.482	0.94	0.706	1	1	0	0	1
15200	*Lanius excubitor*	0.56	1.208	0.619	2.14	2.083	1	1	0	0	1
15230	*Lanius senator*	0.703	1.029	NA	0	1.705	0	1	0	0	1
15390	*Garrulus glandarius*	2.419	0.655	0.855	0.426	0.627	1	0	0	0	0
15430	*Perisoreus infaustus*	2.17	0	0	0.936	0.542	1	0	0	0	0
15470	*Cyanopica cyana*	1.437	0.754	NA	0	1.149	1	0	0	0	0
15490	*Pica pica*	0.38	1.257	2.743	0.454	0.356	0	0	1	0	0
15570	*Nucifraga caryocatactes*	1.302	0.289	NA	0	4.321	1	0	0	0	0
15580	*Pyrrhocorax graculus*	0.267	0.127	0	0	4.588	0	0	0	0	1
15590	*Pyrrhocorax pyrrhocorax*	0.693	1.067	NA	0	2.138	0	0	0	0	1
15600	*Corvus monedula*	0.421	1.877	1.239	0.401	0.519	0	1	1	0	0
15630	*Corvus frugilegus*	0.239	3.158	0.59	0.492	0.407	0	1	1	0	0
15670	*Corvus corone*	0.568	1.694	1.376	0.434	0.461	1	1	0	0	0
15720	*Corvus corax*	1.575	0.754	0.311	0.947	1.556	1	0	0	0	1
15820	*Sturnus vulgaris*	0.385	1.565	2.098	0.486	0.235	0	1	1	0	0
15830	*Sturnus unicolor*	0.411	2.115	0.995	0	0.81	0	1	1	0	0
15910	*Passer domesticus*	0.39	1.277	2.711	0.235	0.362	0	1	1	0	0
15920	*Passer hispaniolensis*	NA	3.614	NA	0	0.974	0	1	1	0	0

15980	*Passer montanus*	0.428	2.291	1.18	0.631	0.161	0	1	1	0	0
16040	*Petronia petronia*	0.457	2.65	NA	0	0.662	0	0	0	0	1
16360	*Fringilla coelebs*	2.209	0.802	0.564	0.479	0.651	1	1	0	0	0
16380	*Fringilla montifringilla*	4.028	0.025	NA	2.707	1.794	1	1	0	0	0
16400	*Serinus serinus*	0.563	1.157	1.373	0.419	1.611	1	1	1	0	0
16440	*Serinus citrinella*	1.464	0.44	0	0	1.676	1	0	0	0	1
16490	*Carduelis chloris*	0.547	1.457	2.03	0.336	0.311	1	1	1	0	0
16530	*Carduelis carduelis*	0.526	1.781	1.088	0.35	0.629	1	1	0	0	0
16540	*Carduelis spinus*	5	0.145	0.18	1.133	0.805	1	0	0	0	0
16600	*Carduelis cannabina*	0.353	2.457	0.509	0.519	0.879	0	1	0	0	1
16630	*Carduelis flammea*	3.674	0.169	0.242	1.462	3.118	1	0	0	0	1
16660	*Loxia curvirostra*	4.774	0.153	0.191	0.914	1.396	1	0	0	0	0
16680	*Loxia pytyopsittacus*	2.373	NA	0	1.733	0.725	1	0	0	0	0
16790	*Carpodacus erythrinus*	1.885	0.866	1.21	0.73	0.491	0	1	0	1	0
17100	*Pyrrhula pyrrhula*	2.081	0.749	0.622	0.555	0.934	1	0	0	0	0
17170	*Coccothraustes coccothraustes*	2.771	0.664	0.66	0.283	0.366	1	1	0	0	0
18470	*Calcarius lapponicus*	0.117	0	0	NA	4.941	0	0	0	1	1
18500	*Plectrophenax nivalis*	NA	0	0	0	5	0	0	0	0	1
18570	*Emberiza citrinella*	0.921	2.014	0.396	0.344	0.333	1	1	0	0	0
18580	*Emberiza cirlus*	0.864	1.622	0.412	0	0.683	0	1	0	0	1
18600	*Emberiza cia*	1.377	0.509	NA	0	1.701	0	0	0	0	1
18660	*Emberiza hortulana*	0.475	2.484	NA	0	0.938	0	1	0	0	1
18730	*Emberiza rustica*	1.308	0	0	1.248	1.203	1	0	0	1	0
18770	*Emberiza schoeniclus*	0.567	0.876	0.395	4.404	1.192	0	0	0	1	0
18820	*Miliaria calandra*	0.447	2.662	0.224	0.326	1.377	0	1	0	0	1

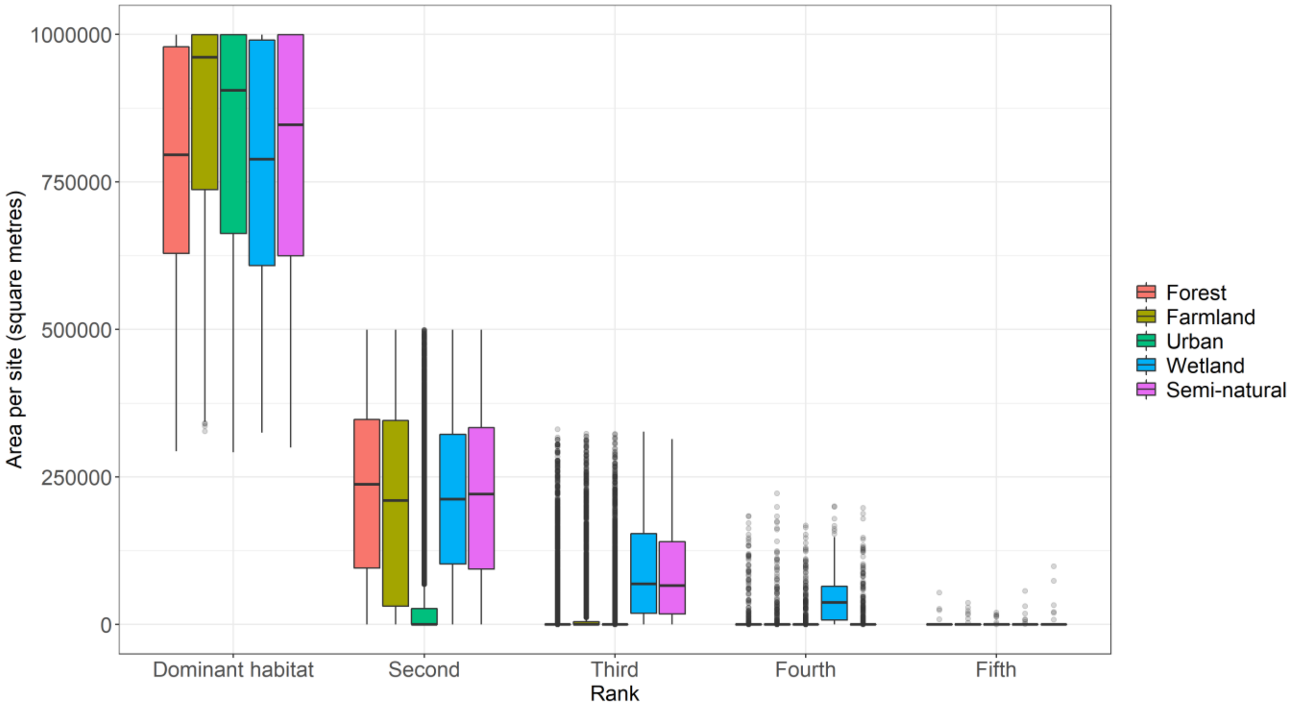


Fig. A.2.1. Area (square metres) for habitats ranked as either the dominant habitat, second, third, fourth or fifth largest area based on total area of the habitat in each site. Habitats are grouped according to their rank based on total area per site.

Table A.2.3. Kruskal-Wallis and post-hoc Dunn's tests examining the influence of reported degree of habitat specialisation on RHU. Separate models were run for each habitat, with species grouped according to whether they were reported in the species-habitat linkage database (Roscher *et al.*, 2015) as being only associated with that habitat, associated with that habitat and one other, associated with that habitat and two others, or not reported as associated with that habitat.

	Focal habitat				
Reported degree of habitat specialisation	**Forest**	**Farmland**	**Urban**	**Wetland**	**Semi-natural**
	chi^2 = 106.65 df = 3 **p < 0.001**	chi^2 = 68.604 df = 3 **p<0.001**	chi^2 = 40.728 df = 3 **p<0.001**	chi^2 = 118.66 df = 3 **p<0.001**	chi^2 = 60.591 df = 3 **p<0.001**
Focal habitat only vs Focal plus one	Z = 2.918 **p = 0.002**	Z = 1.345 p = 0.089	Z = 1.009 p = 0.156	Z = 2.392 **p = 0.008**	Z = 2.435 **p = 0.007**
Focal habitat only vs Focal plus two	Z = 3.928 **p < 0.001**	Z = 3.380 **p < 0.001**	Z = 0.929 p = 0.176	Z = 0.865 p = 0.194	Z = 0.779 p = 0.218
Focal habitat only vs No focal habitat use	Z = 9.522 **p < 0.001**	Z = 4.477 **p < 0.001**	Z = 2.660 **p = 0.004**	Z = 9.106 **p < 0.001**	Z = 5.533 **p < 0.001**
Focal plus one vs Focal plus two	Z = 1.773 **p = 0.038**	Z = 3.650 **p < 0.001**	Z = -0.047 p = 0.481	Z = -0.905 p = 0.183	Z = -1.647 **p = 0.05**
Focal plus one vs No focal habitat use	Z = 6.370 **p < 0.001**	Z = 7.378 **p < 0.001**	Z = 5.066 **p < 0.001**	Z = 6.683 **p < 0.001**	Z = 4.865 **p < 0.001**
Focal plus two vs No focal habitat use	Z = 2.347 **p = 0.009**	Z = 1.209 p = 0.113	Z = 3.408 **p < 0.001**	Z = 5.237 **p < 0.001**	Z = 5.015 **p < 0.001**

Table A.2.4. Total number of sites of each dominant habitat type at a Pan-European level.

Dominant habitat	Number of sites
Forest	5250
Farmland	10,907
Urban	2406
Wetland	1244
Semi-natural	2081

Chapter Three: Quantitative niche-based framework for developing biodiversity indicators: updating the European Forest Bird Indicator

3.1 Abstract

Biodiversity indicators are used to monitor the state and effects of human activity on ecosystems, and biodiversity's response to conservation policies. For an indicator to be policy-relevant it must have a defined purpose, be representative of wider biodiversity across spatiotemporal scales and respond to environmental changes. Due to strong environmental gradients causing spatial variation in species-habitat relationships, broad-scale indicators adopted at lower regional and national levels ("top-down"), potentially fail to address these spatial differences. As an alternative, a "bottom-up" approach sees indicators developed at smaller spatial scales and then integrated to larger scales. Alternatively, indicators can be produced specifically for a given spatial scale ("direct" indicators). As indicator species selection methods can vary spatially, it may be difficult to compile comparable data for "bottom-up" indicators or compare "direct" indicators across spatial scales. Here, we explore the implications for species composition and indicator trends when adopting a "direct", "top-down" or "bottom-up" approach to developing multi-species bird indicators at national, regional and European scales. We explore this using an objective, quantitative process which chooses species for an indicator based on resource use, thereby ensuring that the indicator is sensitive to changes in the environment. We focus on indicators for Europe's forest birds as European forests face ongoing and increasing pressure from climatic and anthropogenic related issues. Furthermore, studies have found that the current European Forest Bird Indicator shows gaps in resource coverage, suggesting that it may not be appropriately sensitive to environmental changes. We show that although species composition of indicator sets for a given spatial scale varied according to the species' selection protocol imposed, overall index trends were broadly comparable. However, "top-down" and "bottom-up" indicators were less representative of the wider community and were likely to be less responsive to environmental change compared to "direct" indicators. We recommend that an objective, standardised

protocol such as the one used in this study be adopted when developing multi-species indicators, and that a “direct” approach is used when selecting the scale at which species are chosen for the indicator.

3.2 Introduction

Global scale biodiversity losses are inherently linked to a range of anthropogenic activities, including the conversion and loss of natural habitats (Fastré *et al.*, 2020) and the overexploitation of natural resources (Reyers and Selig, 2020). In recent decades, a range of biodiversity indicators have been adopted from the national to the global scale to track the effects of these activities on ecosystems (Cairns *et al.*, 1993), monitor biodiversity’s response to conservation management (Butchart *et al.*, 2010), and track progress towards policy targets (Mace *et al.*, 2018). These indicators aim to simplify the results of complex processes occurring within habitats so that they can be more easily interpreted (Niemeijer and de Groot, 2008). As a result, indicators have become essential within conservation policy, environmental management and sustainable development (Niemeijer and de Groot, 2008; Butler *et al.*, 2012; Bal *et al.*, 2018).

For a biodiversity indicator to remain robust and relevant to policy, it must be representative of the wider ecological community across broad spatiotemporal scales and responsive to environmental changes (Zettler *et al.*, 2013; Stevenson *et al.*, 2021). However, indicator species choice differs across spatial scales due to variation along environmental gradients and across biogeographical regions in habitat-biodiversity relationships (Zettler *et al.*, 2013). Therefore, “top-down” indicators, which are produced at broad spatial scales and adopted at the regional and national levels may potentially be insensitive to variation in species’ habitat associations (Knight and Cowling, 2007). As an alternative, “bottom-up” indicators, produced at finer spatial scales which are integrated and projected to larger scales (Fraser *et al.,* 2006; Feld *et* *al.,* 2009) could be used, as they can account for these spatial differences. In addition, "direct" indicators which are produced for a specific spatial scale, take species' habitat associations at the given scale into account (Feld *et al.,* 2009; Terrigeol *et al.,* 2022). However, due to spatial variation in species' selection methods and patchiness in survey coverage, it may be difficult to collect sufficient, comparable and reliable data across all local scale habitats to produce "bottom-up" indicators (Roux *et al*., 2016). In addition, it may be challenging to compare "direct" indicators across spatial scales if the same species are not used in the indicator (Remme *et al*., 2016). The general consensus is that while a set list of species in a "top-down" indicator allows for comparisons to be made across spatial scales, "bottom-up" indicators reflect environmental spatial variation and differences in species' habitat use (Fraser *et al.,* 2006; Feld *et al.,* 2009).

Birds are often used as biodiversity indicators due to their sensitivity to environmental changes, well-studied ecology, physiology and behaviours, the relative ease with which they can be monitored, and their wide ranges allowing for comparisons to be made across spatial scales (Gregory *et al.,* 2005; BirdLife International, 2020; Fraixedas *et al.,* 2020). For example, Wild Bird Indices are published by the European Common Bird Monitoring Scheme (PECBMS; https://pecbms.info/), who collect and collate national indices for breeding bird species across Europe (Brlík *et al*., 2021). Trends generated from these indices monitor European and regional populations of common and widespread breeding birds in Europe. In addition, the European Wild Bird Indices for farmland and forest track changes in the population trends of groups of indicator species associated with these habitats. Most notably, the Farmland Bird Index has monitored a steady decline in farmland bird populations across Europe with an increase in agricultural intensification over the past four decades (Donald *et al*., 2001; Brlík *et al*., 2021). In contrast, the Forest Bird Index has remained relatively stable over time (Forest Europe, 2019; Gregory *et al*. 2019; Brlík *et al*., 2021) despite forest area increasing in Europe. This has mostly been due to forest expansion following agricultural land abandonment (Palmero-Iniesta *et al*., 2021) and changes in forest management which have increased forest area and volume of growing stock (Schelhaas *et al*., 2003). Due to ongoing natural disturbances (Schurman *et al*., 2018), pressures from climate change (Seidl *et al*., 2020) and political challenges (Sotirov *et al*., 2021) all putting greater pressure on forest ecosystems and provision of ecosystem services, Forest Europe, who are central to European policy for sustainable forest management (Forest Europe, UNECE and FAO, 2011), recently set out to revise and update its European forest indicators. This included suggestions to improve the species selection approach for the Forest Bird Indicator (hereafter FoBI) as studies found that the current FoBI may not be appropriately sensitive to changes in habitat quality or resource availability (Wade *et al*., 2014; Forest Europe, 2019). In addition, the current indicator species selection approach for the FoBI relies, to some extent, on expert ornithologist opinion (Gregory *et al*., 2005, 2008; Forest Europe, 2019). This is a relatively straight-forward method for choosing indicator species, however, as with any expert-based assessment, it risks introducing some element of subjectivity and bias due to individual opinions and backgrounds (Forest Europe, 2019; Gregory *et al*., 2019). Studies have found that quantitative methods, which implement an objective species selection criteria framework, offer a beneficial and unbiased approach to choosing indicator species (Fraixedas *et al.*, 2020). Whether expert opinion or a quantitative approach is used, it is vital that species selection is based on ecological principles and that the index has a defined purpose (Gregory *et al.*, 2019) as species choice strongly affects indices' trends (Fraser *et al.*, 2017; Gregory *et al.*, 2019).

Butler *et al.,* (2012) presented an alternative method for indicator species selection whereby species are systematically chosen based on their resource requirements. For this approach, two rules are imposed; all resource types used by the wider community must be covered by at least one of the species in the indicator set and the indicator must be comprised of the most specialised species possible, with each species' specialisation scored according to the number of resource types it uses and its reliance on the target habitat to provide those resources. This ensures that the indicator is representative of the wider community and is sensitive to any changes in land use or resource availability (Butler *et al*., 2012; Wade *et al*., 2014; Magg *et al*., 2019), thereby meeting the key requirements of a reliable indicator (Carignan and Villard, 2002; Failing and Gregory, 2003; Gregory and van Strien, 2010). This niche-based framework has therefore been identified as a suitable method for further consideration in the development of an updated European FoBI (Forest Europe, 2019).

At present the niche-based framework still relies, to some extent, on expert-based opinions as they have been used to determine the candidate species pool from which indicator species were chosen and to quantify each species' reliance on the target habitat (Butler *et al*., 2012; Wade *et al*., 2014). Replacing these steps with objective criteria would remove additional subjectivity from the species selection process. One such approach is to score species' reliance on a given habitat based on their Relative Habitat Use (RHU; Larsen *et al*., 2011), calculated as its abundance in the target habitat, relative to its mean abundance across all other habitats, weighted by habitat availability. O'Reilly *et al.,* (2022) found that RHU produces similar conclusions to literature-based classifications when defining species' association with a habitat. However, RHU is more robust as it is driven by species' abundances and can be calculated at any spatial or temporal scale, if the underlying data are available. In addition, species' RHU scores for a target habitat can be compared to one another so those with the strongest association can be considered for inclusion in the indicator (O'Reilly *et al.,* 2022). Note that expert opinion can also be updated temporally and spatially, and compared across species, however this process is an inefficient use of time and resources (Sutherland and Burgman, 2015) in comparison to RHU.

In this study, we integrate RHU and the niche-based framework to produce a quantitative, objective approach to indicator species selection, and explore the implications for species composition when adopting a “direct”, “top-down” or “bottom-up” approach to producing FoBIs at national, regional and European scales. We use species’ RHU scores for forest habitat both to systematically choose species for the candidate species pool and to quantify each species’ reliance on forest habitat. We explore differences in multi-species indices (hereafter MSI) trends of FoBIs for each spatial scale generated from “direct”, “top-down” and “bottom-up” approaches and compare the trends of the European and regional indices derived using these approaches with equivalent index trends for the current FoBI.

3.3 Methods

3.3.1 RHU calculation

RHU scores for each species were calculated at the European, regional and country levels following O’Reilly *et al.,* (2022). In brief, we used annual, site-level count data for European common breeding birds (168 species) collected between 1998 and 2017 across 22 countries (Table A.3.1). This time frame was used to ensure coverage from a representative suite of countries. Sites were surveyed using either point counts, line transects or territory mapping (Brlík *et al.,* 2021). Each survey site was classified according to the dominant habitat type (forest, farmland, urban, wetland and semi-natural) within a 1km^2 circular area centred on it. Habitat information was derived from Corine Land Cover 2012 (Copernicus Land Monitoring Service, 2012) (Table A.3.2). Defining sites by the dominant habitat type assumes that a large proportion of a species population is likely to be influenced by processes and management associated with that dominant habitat (O’Reilly *et al.*, 2022). For each species, annual RHU scores were calculated for each of the five habitat types in each country, each region and at the European level.

Species' RHU scores in any given year can be sensitive to changes in the number of sites where that species was recorded, especially if the total number of sites where it occurred is small (O'Reilly *et al.*, 2022). RHU scores were therefore only calculated for a given species, in a given year, if that species was recorded in at least 35 sites in that year and only calculated for an individual habitat in a given year if the species was recorded in at least seven sites of that habitat type in that year. These site thresholds also had to be met in at least three years for a species to be included (O'Reilly *et al.*, 2022). Site threshold requirements were the same when calculating RHU scores at European, regional and national levels, to ensure reliable RHU scores were calculated at each spatial scale.

Limited data availability prevented national RHU score calculations for Latvia and Greece. However, count data from these countries were included in calculations of species' regional and European RHU scores. In addition, East and West Germany data were combined when calculating species' RHU scores at the national level. The PECBMS splits Germany into East and West for the Central & East and West PECBMS regions respectively. Combining data in this way allowed us to produce an indicator set for Germany as a whole.

3.3.2 Candidate species pool and resource requirements matrix

For each country, region, and at the European scale in turn, we identified a candidate indicator species pool, selecting all species with RHU scores ≥1 for forest habitat in at least 50% of the years in which RHU scores were generated for them at the target spatial scale (Fig. 3.1; Step 1). No species met this threshold in Cyprus or Slovenia, therefore candidate species pools were not produced for these countries. In addition, as Cyprus and Slovenia are the sole countries to represent the East Mediterranean and West Balkan regions respectively in this study, candidate species pools were not generated for these regions (Table A.3.1).

A resource requirements matrix for forest habitat was constructed (Fig. 3.1; Step 2) and fit to each candidate species pool. This matrix covered summer and winter diets, forest foraging habitat, nest type and nesting habitat, with a simple binary code (0/1) defining each species' use of each resource type within these categories (Snow *et al.*, 1998; Hořák and Storchová, 2018) (Table A.3.3, A.3.4). For the derived indicators to be sensitive to changes in the availability of forest-specific resources, species identified as either having a predominantly aquatic diet or as not nesting in forest habitats were subsequently removed. Finally, we categorised each species in each candidate species pool as either resident or migrant (short- or long-distance migrant) to the target spatial scale (BirdLife International and Handbook of the Birds of the World, 2019). These categories were used to determine the number of resources available to each species at the target spatial scale, with a total of 124 possible resource combinations available for resident species (summer and winter diet resources plus nesting resources) and 70 for migratory species (winter diet resources excluded).

For each species, we calculated the number of resources used as a percentage of the total number of resources available to it and rounded this to the nearest whole number, as the species selection software, *Specsel*, (Wade *et al*., 2014) only accounts for integers for number of resources used. We also calculated each species reliance on forest habitat as its mean RHU for forest across all years where RHUs were available. Each species' sensitivity score was then calculated as the percentage of resources used divided by its reliance on forest habitat (*i.e.,* mean forest RHU) at the given spatial scale. Lower scores were therefore assigned to species assumed to be more sensitive to changes in resource availability in forest habitats (few resources used and/or higher forest mean RHU) and higher values to species assumed to be less sensitive (many resources used and/or lower forest mean RHU) (Butler *et al*., 2012; Wade *et al*., 2014; Teufelbauer *et al.,* 2017; Magg *et al*., 2019).

3.3.3 Indicator species selection

3.3.3.1 “Direct” indicator approach

We applied the species selection algorithm (*Specsel*; Wade *et al*., 2014) to the European, regional and country-specific candidate species pools in turn. For each possible indicator set size (from two species to the number of species included in the candidate species pool) the algorithm identifies all combinations of species that, between them, exploit all resource types used by the wider community (Fig. 3.1; Step 3) and ranks them according to the average sensitivity score across constituent species. From this, we selected the indicator set with the lowest overall average sensitivity (Fig. 3.1; Step 4) *i.e.*, comprised of the most sensitive and specialised species possible. We ran this process at the European level to produce a *European* indicator set, separately for each region to produce *regional* indicator sets and for each country separately to produce *national* indicator sets.

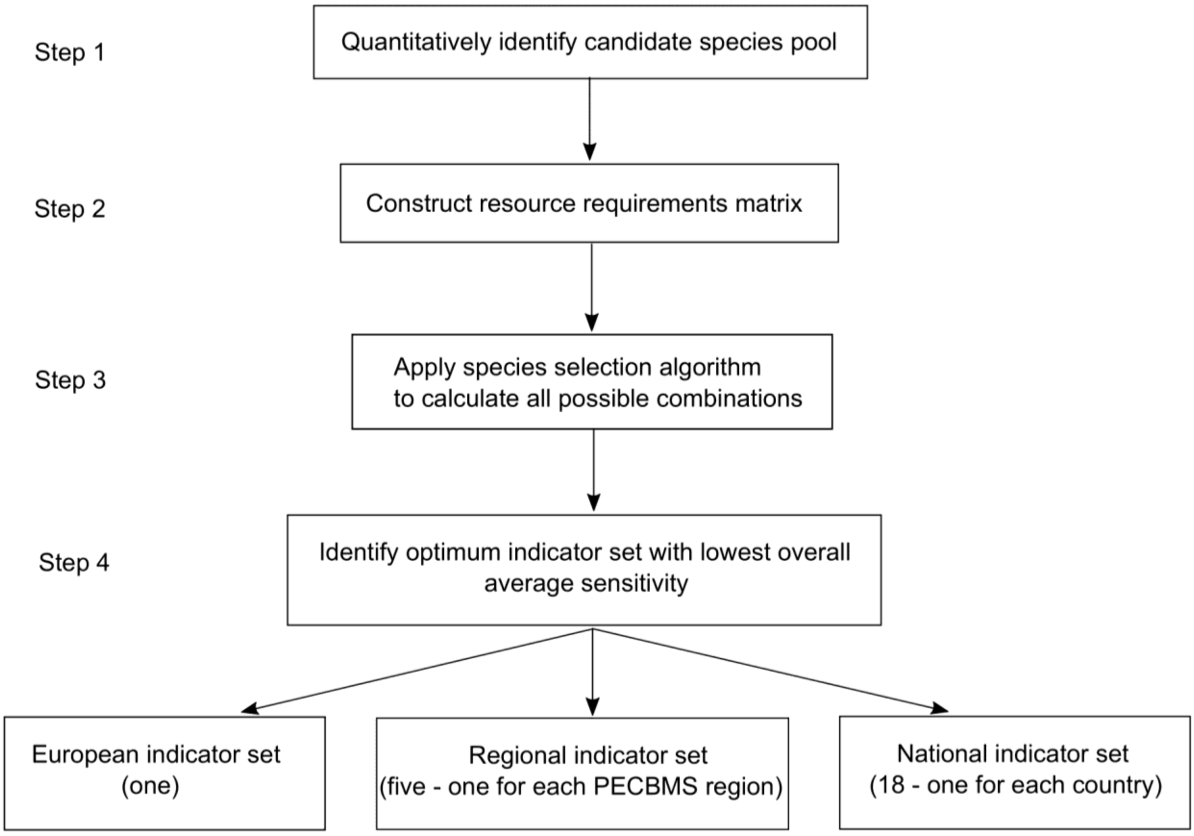


Fig. 3.1. Outline of the niche-based framework for indicator species selection as introduced by Butler *et al.*, (2012). The above process demonstrates the selection of species from a candidate species pool at a given spatial scale that produces an indicator set for that same spatial scale *i.e.* European candidate species pool to produce a single *European* indicator set, a regional candidate species pool to produce a *regional* indicator set (five in total – one for each PECBMS region) and a national candidate species pool to create a *national* indicator set (18 in total – one for each country).

3.3.3.2 “Top-down” indicator approach

For each region in turn, species in the *European* indicator set that were present in that region were assigned to the indicator set for that region (hereafter defined as *European – regional* indicator sets). Next, for each of the 18 countries in turn, species in the *European* indicator set that were present in that country were assigned to that country’s indicator set (hereafter *European – national* indicator sets*)*. Finally, each country was assigned to its corresponding region (Table A.3.1). Then, for each country in turn, species in the corresponding *regional* indicator set that were present in that country were assigned to the indicator set for that country (hereafter *regional – national* indicator sets). Regional indicator sets for Central & East and West regions both contributed to the *regional - national* indicator set for Germany.

3.3.3.3 "Bottom-up" indicator approach

Using the species selection algorithm for each region in turn, "bottom-up" regional indicator sets were selected from composite candidate species pools containing all species selected in the *national* indicator set of any country within that region (hereafter *national – regional* indicator sets). The *national* indicator set from Germany contributed to the *national - regional* indicator sets for both Central & East and West regions. Next, a "bottom-up" European indicator set was selected from a composite candidate species pool containing all species selected in any of the 18 *national* indicator sets (hereafter *national – European* indicator set*)*. Finally, the same process was applied to select a "bottom-up" *regional - European* indicator set from a composite candidate species pool produced by combining *regional* indicator sets.

Species sets for "direct" *European*, *regional* and *national* indicator sets with their corresponding "top-down" and/or "bottom-up" indicators are available in Table A.3.7.

3.3.4 Data analysis

All subsequent analyses were carried out in R version 4.0.1 (R Core Team, 2020).

3.3.4.1 Average sensitivity and resource coverage

For the European, regional and national levels in turn, we explored differences in average sensitivity and resource coverage between “direct”, “top-down” and/or “bottom-up” indicators. The number of resources covered by “top-down” and “bottom-up” indicators were expressed as a percentage of the total number of resources used by species in the “direct” indicator set for a given spatial scale (hereafter referred to as scale-dependent resource coverage). The scale-dependent resource coverage of “direct” indicators was therefore assumed to be 100%. For the regional and country level in turn, Wilcoxon signed-rank tests were carried out to i) test for a difference in average sensitivity between indicator sets and ii) determine if the percentage of scale-dependent resources covered by “top-down” and “bottom-up” indicators were significantly lower than “direct” indicators. As species occurred in more than one indicator set for a given spatial scale, Wilcoxon tests were used as species composition of indicator sets were not independent of one another. Indicator sets were paired for the same region or country. As there were only three indicator sets produced for Europe, statistical comparisons between these could not be made.

3.3.4.2 MSIs

Multispecies indices (MSIs) were calculated using the MSI-tool (Soldaat *et al.*, 2017) for each indicator set at i) the European scale, using the European species indices, ii) at the regional scale, using species indices for each region and iii) at the national scale, using species national level indices for each country. Using the RTRIM-shell package in R (Pannekoek and van Strien, 2001; Bogaart *et al.*, 2020), we used site-level count data to calculate national indices (+/- SE) for each species that occurred in the national level indicator sets for each of the 18 countries between 1998 and 2017. These indices reflect changes in a species' national population between 1998 and 2017. PECBMS provided regional and European level population indices for species that occurred in the regional and European indicator sets respectively. Although count data from 22 out of 28 European countries included in PECBMS were available for this study, the European and regional species' indices provided by PECBMS include national level indices from six countries where site level count data were not available for this study. Therefore, there was some mismatch between the countries that contributed their count data to generating species' RHU scores at the European and regional levels in this study, and the countries that contributed to the European and regional level species indices produced by PECBMS. Species' RHUs at the European and regional levels represent species' forest habitat association at these large spatial scales. Therefore, it is unlikely that count data from these missing countries will significantly change the extent of species' forest habitat association at the European or regional level.

The first index value in the MSI was set to 100 and standard error = 0, with 95% confidence intervals around the yearly indices calculated by resampling individual species indices with replacement 10,000 times, re-calculating the index each time (Buckland *et al.*, 2005). We also used the MSI-tool to calculate smoothed trends (LOESS-regression, span = 0.75, degree = 2) for each indicator in order to best describe the overall population trend, and minimise interannual variation (Buckland and Johnston, 2017; Gregory *et al.*, 2019). To test for significant differences between MSIs for indicator sets at a given spatial scale, the TREND_DIFF function (using 1000 iterations), based on Monte Carlo procedures, was used (Soldaat *et al.*, 2017; Gregory *et al.*, 2019). This calculated the average difference between sets of MSIs with standard error and the significance of that difference.

Finally, we compared “direct”, “top-down” and “bottom-up” regional and European MSIs to the current corresponding FoBI using the TREND_DIFF function. Note that species composition for the current regional FoBIs are a subset of the species in the European FoBI (i.e. “top-down”; https://pecbms.info/). This comparison was not generated for the Southeast region as PECBMS do not produce a FoBI for this region.

3.4 Results

3.4.1 Species in indicator sets

62 species occurred in the niche-based indicators across the European, regional and national levels. The average set size for European indicators was 25.67 ±0.88 species, 18.13 ±1.25 species for regional indicators and 13.17 ±0.73 species for national indicators (Fig. 3.2). The most frequently selected species were Jay (*Garrulus glandarius*), followed by Goldcrest (*Regulus regulus*) and Coal tit (*Periparus ater*). 16 species in the current European FoBI occurred in at least two of the niche-based European indicators, with 14 of these occurring in all three indicators (*European, regional - European, national - European*), whilst 18/34 species in the current FoBI did not occur in any of the European niche-based indicators. At the regional level, 13/24, 13/25, 15/27 and 15/29 species in the North, South, Central & East and West current FoBIs respectively occurred in at least one of the niche-based indicators for the corresponding region (Fig. 3.2).

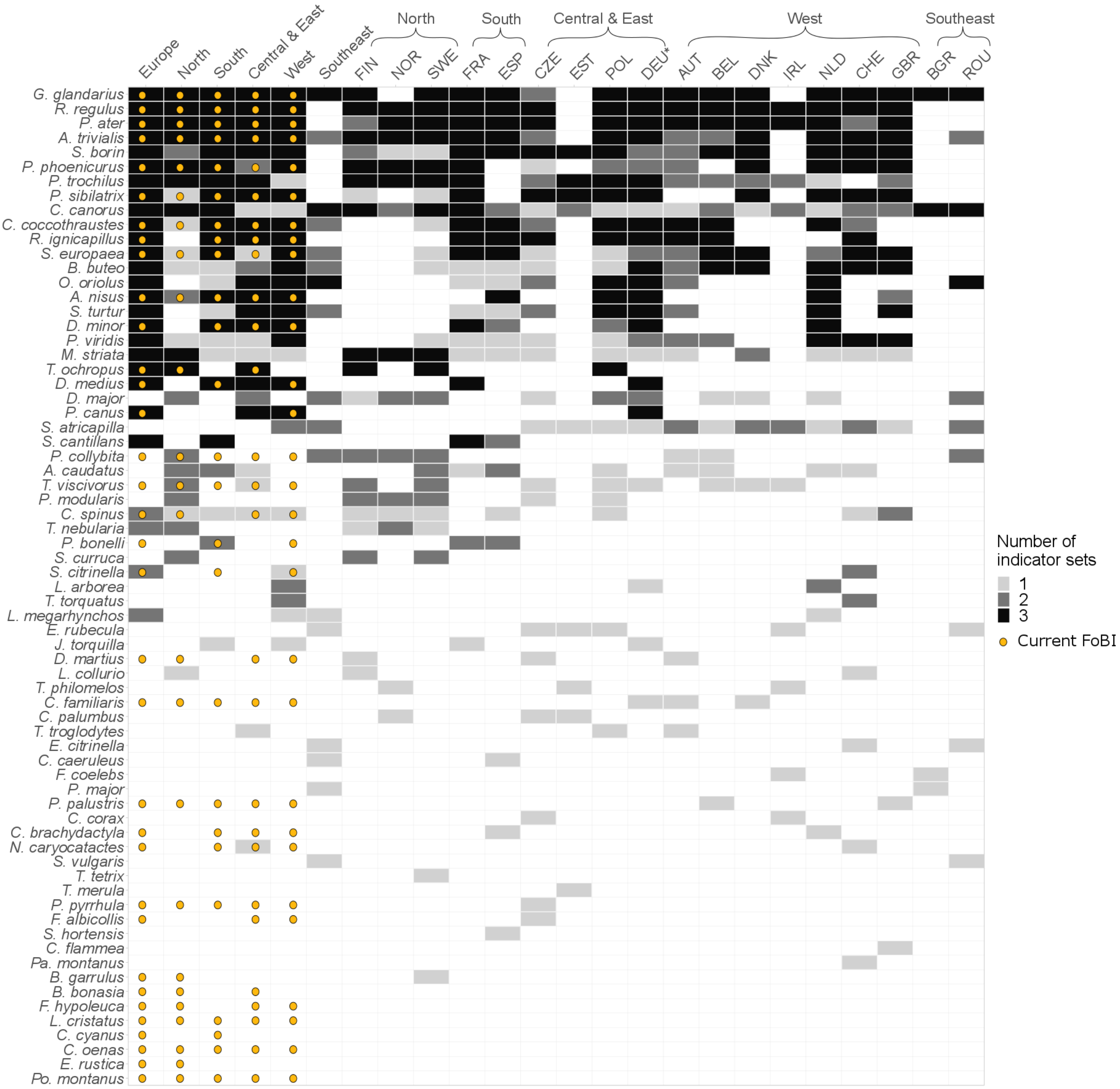


Fig. 3.2. Frequency of each species occurrence across indicator sets for Europe, for each region and each country. Countries are given a three-letter code (Table A.3.5) with species full names provided in Table A.3.6. Here, species can occur in a maximum of three indicator sets and a minimum of one indicator set at each spatial scale. For comparison, species that occur in the current European FoBI are also identified. *DEU: *regional* - *national* indicator set is derived from both the Central & East and West regions. Equally, the national German indicator set contributes to both the Central & East and West *national* - *regional* indicator sets.

3.4.2 Average sensitivity and resource coverage

At both the national and regional levels, “direct” indicators had lower sensitivity scores than either “top-down” or “bottom-up” indicators, with these differences significant at the national level. The exception to this overall pattern was found in the South region where the *national - regional* indicator had the lowest average sensitivity compared to its *European - regional* or *regional* indicators (Fig. 3.3, Table 3.1). At the European level, the *national - European* set had the lowest average sensitivity (4.84 ±1.108), followed by the *European* indicator (4.87 ±1.151) and *regional - European* (4.95 ± 1.246).

Indicator sets at the European level each covered 100% of scale-dependent resources, while at the regional level, there were no significant differences between indicator sets for the percentage of scale-dependent resources covered. However, at a national level, the percentage of scale-dependent resources covered by *European - national* (92.39 ± 7.22) and *regional - national* (93.28 ± 7.38) indicator sets were significantly lower than their corresponding *national* indicators (103.78 ± 2.77) (Fig. 3.3, Table 3.1).

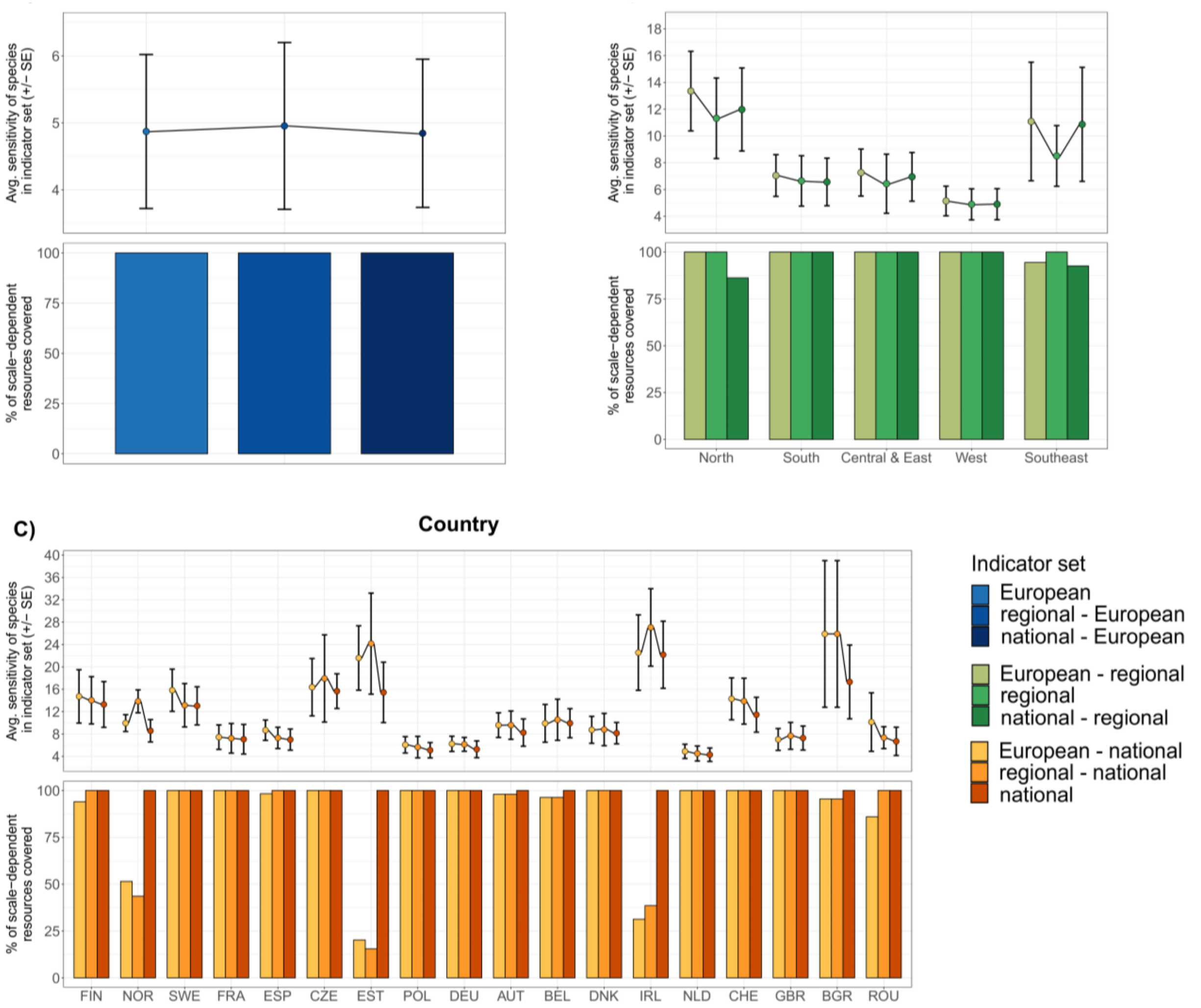


Fig. 3.3. Upper graph in A, B and C shows the average sensitivity (± SE) across species in each indicator. Each species' sensitivity is calculated as the number of resources used as a percentage of the total number of resources available, divided by the species' mean Relative Habitat Use for forest (*i.e.*, quantitative metric for the extent of habitat association). Lower graph in A, B and C shows the number of resources covered by indicators for each spatial scale expressed as a percentage of the total number of resources used by species in the "direct" indicator set (*European*, *regional*, *national*) for that same spatial scale (referred to here as scale-dependent resource coverage). The scale-dependent resource coverage of "direct" indicators was therefore assumed to be 100%. Each country is denoted by a three-letter code (Table A.3.5).

Table 3.1. Wilcoxon signed-rank test results for the difference in average sensitivity and percentage of scale-dependent resources covered by species in each indicator. Indicator sets were paired for the same region or country. Significant values are highlighted in bold.

		European - regional vs regional	***regional vs national - regional***	***European - regional vs national - regional***
Region	Average sensitivity	V= 15, p = 0.063	V= 2, p = 0.188	V= 15, p = 0.063
	Percentage of scale-dependent resources covered	V = 0, p = 1	S = 3, p = 0.371	S = 3, p = 0.371
Country		***European - national vs national***	***regional - national vs national***	***European - national vs regional - national***
	Average sensitivity	**V= 168, p < 0.001**	**V= 171, p < 0.001**	V= 86, p = 1
	Percentage of scale-dependent resources covered	**V = 0, p = 0.009**	**V = 0, p = 0.036**	S = 7, p = 0.529

3.4.3 MSIs

3.4.3.1 European

The three European indicator MSIs (*European, regional* - *European* and *national* - *European*) have remained stable over time (Fig. 3.4, Table 3.3, Table A.3.8), with no significant differences between them (Table A.3.9) or compared to the current FoBI (Table A.3.10).

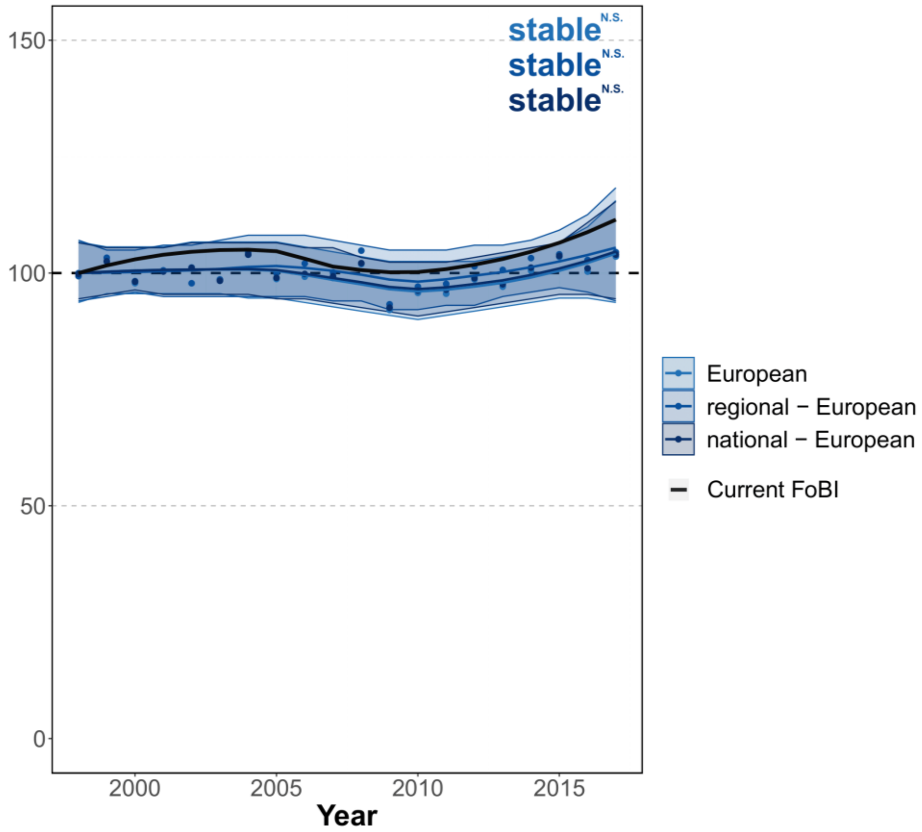


Fig. 3.4. Smoothed European multi-species indices (MSIs), with shaded 95% confidence intervals for forest birds with species selected according to an objective species selection algorithm. The candidate pools from which species were selected were derived directly from a European candidate species pool (*European*) or from "bottom-up" regional (*regional* - *European*) or national level (*national* - *European*) approaches (coloured lines). The black line shows the current Forest Bird Indicator for comparison. Indices were set to 100 and their SEs to 0 in 1998. Description of the overall trend for the *European, regional* - *European* and *national* - *European* indicators are provided in the upper right corner with significance of the trend, N.S., not significant.

3.4.3.2 Regional

In general, regional level MSIs were stable regardless of species selection approach. However, the *regional* index for Southeast shows a significant moderate increase, while the *European - regional* trend for West shows a significant moderate decline (Fig. 3.5, Table A.3.8). There were no significant differences between MSIs for indicators within any region (Table A.3.9) except in the West where the current FoBI was significantly more positive than its corresponding *European - regional* indicator (Table A.3.10).

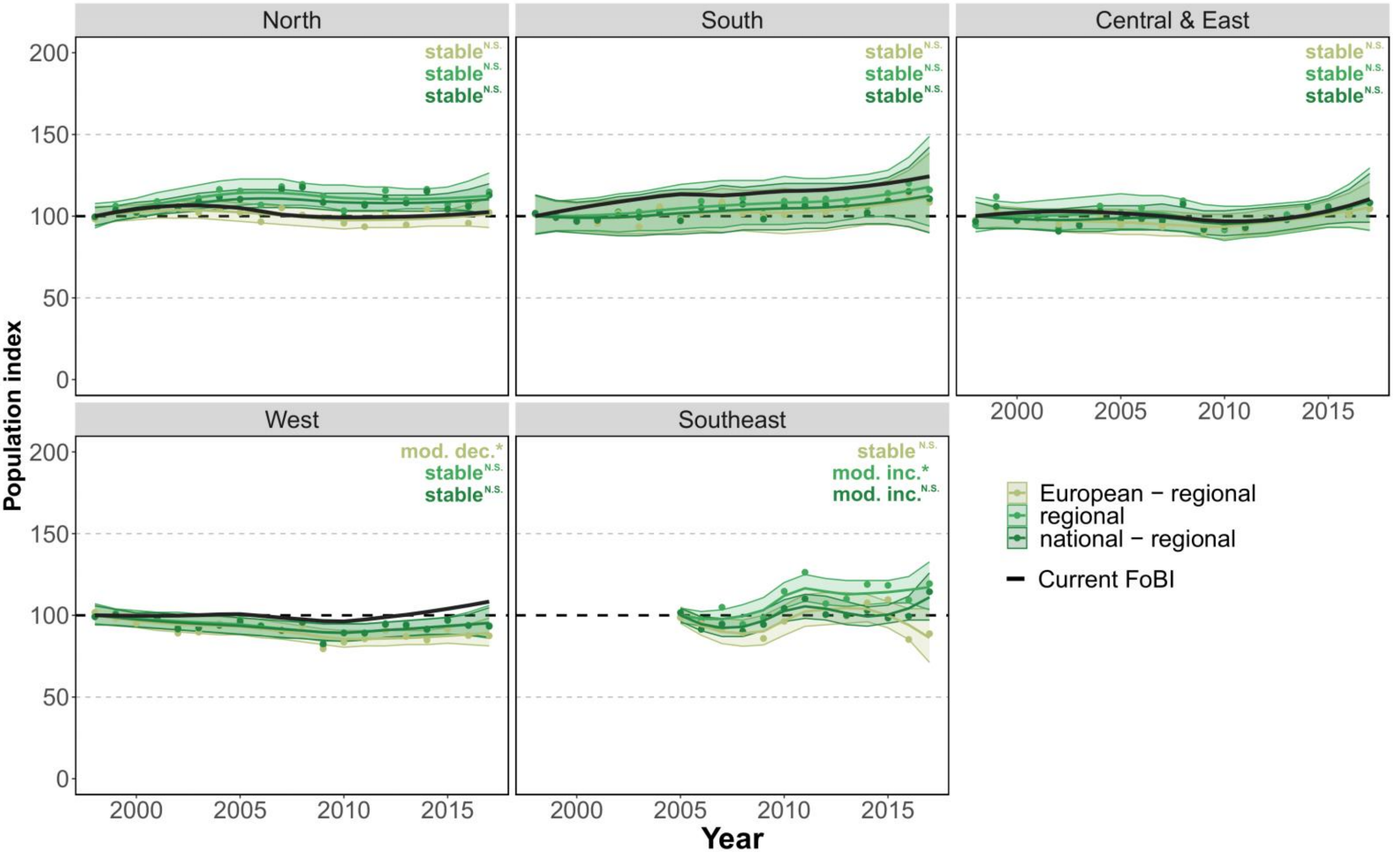


Fig. 3.5. Smoothed regional multi-species indices (MSIs), with shaded 95% confidence intervals for forest birds with species selected according to the niche-based framework. The candidate pools from which species were selected were derived directly from a regional candidate species pool (*regional*), from a “top-down” European approach (*European - regional*) or from a “bottom-up” national approach (*national - regional*) (coloured lines). *National - regional* indicator set from Germany contributed to the indicator sets for both

Central & East and West regions. The black line shows the current Forest Bird Indicator (FoBI) for comparison where available. Indices were set to 100 and their SEs to 0 in 1998 for North, South, Central & East and West, and in 2005 for Southeast. Description of the overall trend for the *European* - *regional, regional* and *national* - *regional* indicators are provided in the upper right corner with significance of the trend; p<0.05, *, not significant, N.S.

3.4.3.3 National

Overall, MSIs for indicators within each country demonstrated similar trends regardless of the selection approach (*European* - *national, regional* - *national, national*). The exceptions to this were Finland and the Czech Republic. In Finland, the *European – national* index had a significant moderate decline and the *regional – national* and *national* indices had significant moderate increases, while in the Czech Republic, the *European – national* and *regional – national* indices had significant moderate declines and the *national* index had a significant moderate increase (Fig. 3.6, Table A.3.8). When comparing MSIs within each country, there were significant differences within eight of the 18 countries (Table A.3.9).

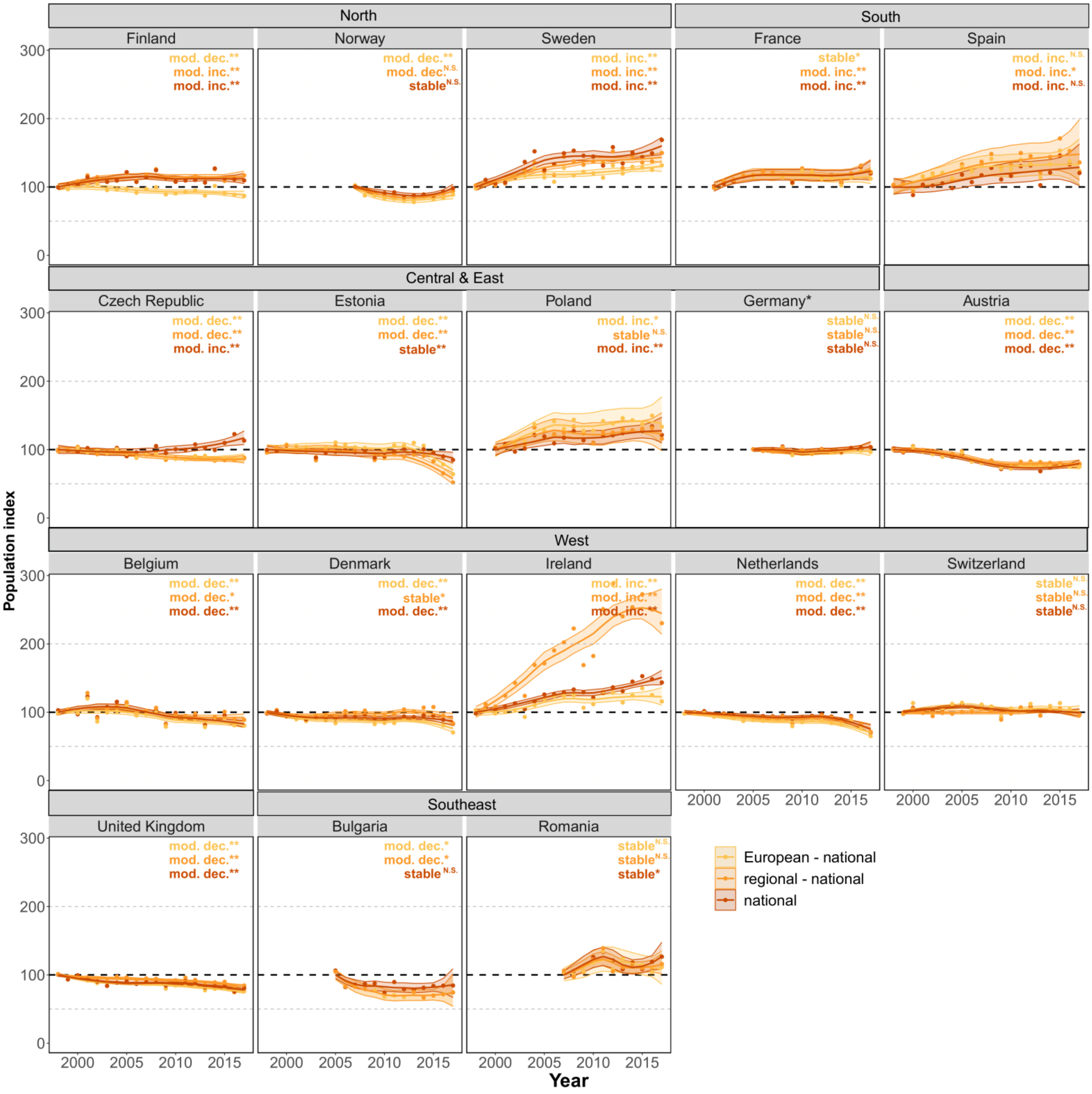


Fig. 3.6. Smoothed country level MSIs, with shaded 95% confidence intervals for forest birds with species selected according to the niche-based framework. The candidate pools from which species were selected were derived directly from a national level candidate species pool

(*national*) or from a "top-down" European (*European – national*) or regional (*regional – national*) approach (coloured lines). **regional – national* indicator set for Germany was derived from the indicator sets produced for the Central & East and West regions which were aggregated together. Indices were set to 100 and their Ses to 0 in the first year data was available for each given country. Description of the overall trend for the *European - national, regional – national* and *national* indicators are provided in the upper right corner with significance of the trend; p<0.01, **, p<0.05, *, not significant, N.S.

3.5 Discussion

Although "direct", "top-down" and/or "bottom-up" indicators for a given spatial scale comprise of different suites of species, the resultant MSIs generally show similar temporal trends for each spatial scale. However, "direct" indicators are composed of more specialised species, and cover more resources at the given spatial scale compared to "top-down" and "bottom-up" indicators, suggesting that "direct" indicators will be more sensitive to any future changes in resource availability. At European and regional levels, niche-based indicators showed similar trends to current FoBIs, despite differences in species composition, with the exception of the West region. However, niche-based indicators were composed of more specialised species and covered the same, if not more scale-dependent resources than the current FoBI, despite fewer species in the niche-based indicator set lists. This suggests that niche-based indicators are representative of wider biodiversity and are more sensitive than the current FoBI to changes in resource availability.

3.5.1 Comparing "top-down", "bottom-up" and "direct" indicators

At a national level and in the Southeast region, "top-down" niche-based indicators are composed of less specialised species and cover fewer scale-dependent resources compared to "direct" indicators. Although "top-down" indicators can provide a general overview for forest bird community health, conservation and management are more often applied at smaller spatial scales (Wade *et al.*, 2014). Furthermore, spatial differences in forest cover (Basile *et al.*, 2021) and composition, scale of forest fragmentation, availability of forest in the surrounding landscape and extent of management practices (Balestrieri *et al.*, 2015; Czeszczewik *et al.*, 2015) impact species' spatial distribution and abundances (Balestrieri *et al.*, 2015; Basile *et al.*, 2021; Hofmeister *et al.*, 2017). Therefore "top-down" indicators may be less sensitive than "direct" indicators to spatial variation in forest bird community structure which are shaped by the above processes. Greater resource coverage and more sensitive suites of species in "direct" indicators further suggest that these indicators would monitor forest bird communities in greater detail as they account for context-dependent forest habitat reliance and are sensitive to resource availability and environmental changes at that scale.

In the North and Southeast regions, "bottom-up" *national* - *regional* indicators cover fewer scale-dependent resources than the corresponding "direct" indicators. Species in the "direct" *regional* indicators for these regions which cover the additional resources do not occur in the "bottom-up" *national* - *regional* candidate pool because they do not meet the site threshold for RHU calculation at the national level. Meeting the site threshold may be an issue at the finer spatial scale if there are too few monitored sites or if a species is counted in few sites in a given country. Ensuring that more sites are surveyed would reduce the number of species that are removed, however, this is often difficult to achieve due to the cost, time and number of volunteers needed to carry out site monitoring (Juffe-Bignoli *et al.*, 2016). Additionally, if a species is counted in few sites, then it may be too rare for its population to be accurately monitored. Including rare species in an indicator may decrease precision in trend estimates and raise questions over its representativeness of the wider community (Gregory *et al.*, 2019). In this study, we produced indicators and MSI trends based on the 168 common breeding birds in Europe, so issues of species rarity were not encountered. However, a recent study by Korner-

Nievergelt *et al*., (2022) demonstrates how the calculation of MSIs can be modified to account for rare species, those with very low numbers, newly occurring species, and temporarily or permanently disappearing species. Therefore, more studies (see Wade *et al.*, 2014) should explore producing European FoBIs which are derived from candidate pools where all breeding bird species in Europe are considered.

We further find that North and Southeast indicators are composed of less specialised species compared to the other three regions. The Southeast is composed of three countries whose monitoring schemes are small in scale, resulting in fewer monitored sites, more species falling below the site or RHU thresholds, and the final indicators being composed of more generalist species. Including generalists will result in a less responsive indicator to changes in land use or resource availability, as they can switch to exploiting other resources and/or a lower proportion of their resources are affected (Norris and Harper, 2004; Wade *et al*., 2014). Increasing the number of sites surveyed in this region may ensure more species are included but, as previously outlined, this is often not straightforward. Despite the fact that forest dominated sites make up 64% of all surveyed sites in the North, species in indicator sets for this region generally have lower forest RHU scores than species in indicator sets for other regions. In addition, the proportion of forest found in sites classified as being dominated by farmland, urban and wetland habitat are higher in the North than in any other region (Fig. A.3.1). Northern Europe is described as a grassland-forest mosaic landscape, with small areas of cropland, open or wooded meadows and pastures (Eriksson, 2016). Thus, farmland, urban and wetland sites in the North where woodland and trees occur are more likely to contain forest species compared to farmland, urban and wetland sites in other regions. This increases species' RHUs for non-forest dominated sites and decreases their RHUs for forest in the North.

3.5.2 Comparing European, regional and national MSI trends

MSIs at the regional and European levels are generally more stable than at the national level as trends for each species in regional and European indicators are represented by the species' average trend across countries within a region or across countries within Europe (Brlík *et al*., 2021). Therefore, regional and European trends are not significantly affected by large annual differences in species indices. In addition, national level indicators have fewer species than indicators at European and regional scales, therefore MSIs are based on a smaller suite of species with more stochastic indices. In 16 of the 18 countries, MSIs either increase moderately or remain stable, or decrease moderately or remain stable. The exception to this is found in Finland and the Czech Republic where two indicator sets within each country have the same MSI trend *i.e.,* both either increase or decrease moderately, and the third has an opposing trend, *i.e.,* moderate decrease or increase. Furthermore, indicator sets within these countries with the same trend have more species in common than either has with the indicator set with the opposing MSI trend. This demonstrates how MSIs will reflect the trend experienced by the majority of species *i.e.,* if more species decline than increase, the MSI will go down and vice versa (Gregory *et al*., 2005). Furthermore, spatial differences in land management strategies and variation in species responses to these practices across Europe also supports results for large differences in MSI trends between countries (Bengtsson *et al.,* 2000; de Groot *et al.,* 2016).

3.5.3 Comparing niche-based indicators and the current Forest Bird Indicator

47% of species in the current European FoBI do not occur in the corresponding European niche-based indicators, and 52% to 56% of species in the current regional FoBIs do not occur in the corresponding regional niche-based indicators. Despite differences in species composition and fewer species in the niche-based indicators, niche-based indicators cover the same, if not more resources than the current FoBI (Table A.3.11). This suggests that there are some redundancies in resource coverage in the current FoBI, as a greater number of species does not result in greater resource coverage. Redundancy in an indicator increases bias towards resources that are exploited by multiple species. Some redundancy in an indicator is important however as without it, the indicator may be sensitive to external factors which it is not designed to indicate *e.g.*, hunting, disease, which affect individual species in the indicator (Wade *et al*., 2014). The niche-based approach therefore allows the indicator to be appropriately reactive to changes in resource availability as all resources are covered, with less redundancy than the current FoBI. Despite differences in species composition and resource coverage, MSIs for niche-based indicators at the European and regional levels do not differ significantly from the corresponding current FoBI. The exception to this is found in the West, where the *European - regional* trend is significantly more negative than the current West FoBI. We find that three species are unique to the *European – regional* indicator; Cuckoo (*Cuculus canorus*), Spotted Flycatcher (*Muscicapa striata*) and Willow warbler (*Phylloscopus trochilus*), and do not occur in the current West FoBI, or the other two niche-based indicators. Moderately declining trends in Europe over the past 30 years for these three species (PECBMS; https://pecbms.info/) suggests that their trends contribute to an overall moderate decline in the indicator’s MSI trend, while fewer species in the other indicators have such significant declines. Although these three species are widespread across the West region (PECBMS; https://pecbms.info/), average sensitivity of the *European – regional* indicator is higher than the *regional* or *national – regional* West indicators (5.14, 4.89, 4.90 respectively). This result, along with previous conclusions regarding the usefulness of the “direct” indicators suggests that the *regional* West indicator MSI trend should be considered most closely.

3.5.4 Study limitations

Differences in survey method between countries may pose a limitation to this study. For example, the United Kingdom, Ireland and Poland use line transects with each individual survey covering two 1 km lengths within a 1 x 1 km square (Risely, 2012; Lewis *et al.,* 2019; “Common Breeding Bird Survey (MPPL)”, 2022), while the Catalonian scheme’s line transect is 3 km in length (“SOCC methodology”, 2022). By contrast, Denmark uses a point count system with 10-20 points per survey, with at least 200 m between points (Vikstrøm *et al.,* 2022), while Spain’s point count scheme is 20 points within a 10 x 10 km square (SEO/BirdLife, 2013). These differences suggest that there may be a disparity between the specific location in which birds are counted and the classification of the dominant habitat for each sampled site. Therefore, species’ RHU scores may be higher than expected for some habitats. However, we find that 82.45% of sites classified by the dominant habitat type in a 25km^2 circular area match the dominant habitat type classified at a 1km^2 circular area. Therefore, if a larger area were used it is unlikely that sites would be classified differently. Therefore, issues of site classification based on the dominant habitat are more likely to arise at smaller spatial scales. To solve for this, we recommend that detailed habitat information be collected during each survey to ensure that habitat classification and location of bird sightings are correlated. This practice is already carried out in some European countries, although currently not in all.

In this study, niche-based forest bird indicators meet a series of general requirements which all indicators should follow; easily measured, sensitive and reactive to ecosystem stressors, respond to stressors in a predictable manner, can be integrated with other indicators and have low variability in its response (Dale and Beyeler, 2001; Gregory *et al*., 2005; Heink and Kowarik, 2010). However, indicator suitability will be established differently for different purposes (Failing and Gregory, 2003) and given the array of purposes, a number of approaches can be applied for developing an indicator (Heink and Kowarik, 2010). Here, we choose to apply the niche-based framework to a matrix of resource requirements which encompass the full forest habitat. This includes forest edge and early-transitional forest habitat types.

However, increased anthropogenic activity in forest habitat in Europe has led to an interest in monitoring biodiversity indicators for larger tracts of forest and old-growth forest (Ćosović *et al.,* 2020). Therefore, our study may be limited in its ability to predict changes in these specific habitat types. Additional exploration finds that even if a more conservative threshold is set prior to producing “direct” indicators at national, regional and European scales, species composition and resultant MSIs generally show similar results (Fig. A.3.2, A.3.4 - A.3.6). Therefore changes in old-growth forest or large expanses of forest are appropriately monitored. However, if forest edge and early-stage specialists are removed from the candidate species pool in order to monitor changes in old-growth forest and/or large forest expanses, then the indicator may be not be sensitive to changes in forest edge or early stage forest resources, as these MSIs showed more positive trends (Fig. A.3.3, A.3.4 - A.3.6). These results suggest that having a clear purpose for the indicator is vital to ensure that overall, the indicator is appropriately sensitive to any changes in resources.

3.6 Conclusion

Although indicators for a given spatial scale generally show similar temporal trends, “direct” indicators cover more scale-dependent resources and have a more specialised suite of species overall compared to “top-down” or “bottom-up” indicators. This suggests that “direct” indicator MSIs will be more sensitive to changes in resource availability. Although species composition of indicator sets across spatial scales vary, each set represents the same resource matrix, and therefore the same stressors on forest ecosystems due to the underlying conceptual framework and objective nature of the species selection process. This allows indicators to be comparable over space and time. If adopted, such “direct” indicators could ensure that land-management and policy decisions are targeted appropriately at all spatial and temporal scales. In addition, niche-based indicators had more specialised species and covered more resources overall compared to the current FoBI suggesting that objective, niche-based indicators are more representative of the wider forest bird community than the current approach and could reduce redundancy in resource coverage.

3.7 Appendices

Table A.3.1. Countries in Europe with corresponding PECBMS region. There were not enough data available to generate species' RHU scores for Latvia and Greece, and no species met the RHU threshold for Cyprus and Slovenia, so final indicator sets were not generated for these countries or for West Balkan or East Mediterranean regions. Species data from Greece and Latvia still contributed to the Southeast and Central & East regions respectively, and species data from Latvia, Greece, Cyprus and Slovenia still contributed to the European scale. *East and West Germany data were combined when calculating RHU scores at the national level for Germany.

Region	**Country**	**Years of site-level count data available**
North	Finland	1998 - 2016
	Norway	2007 - 2017
	Sweden	1998 - 2017
South	France	2001 - 2017
	Spain	1998 - 2016
Central & East	Czech Republic	1998 - 2017
	Estonia	1998 - 2016
	East Germany*	2005 - 2016
	Latvia	2005 - 2016
	Poland	2000 - 2017
West	Austria	1998 - 2017
	Belgium	1998 - 2017
	Denmark	1998 - 2016
	West Germany*	2005 - 2016

	Ireland	1998 - 2016
	Netherlands	1998 - 2016
	Switzerland	1999 - 2016
	United Kingdom	1998 -2017
Southeast	Bulgaria	2005 - 2016
	Greece	2007 - 2016
	Romania	2007 - 2017
West Balkan	Slovenia	2007 - 2017
East Mediterranean	Cyprus	2006 - 2017

Table A.3.2. Corine Land Cover 2012 Levels 1 – 3 with habitat category assigned to each Level 3 habitat

Assigned habitat category	**Level 1**	**Level 2**	**Level 3**
Urban	Artificial surfaces	Urban fabric	Continuous urban fabric
			Discontinuous urban fabric
		Industrial, commercial and transport units	Industrial or commercial units
			Road and rail networks and associated land
			Port areas
			Airports
		Mine, dump and construction sites	Mineral extraction sites
			Dump sites
			Construction sites
		Artificial, non-agricultural vegetated areas	Green urban areas
			Sport and leisure facilities
Farmland		Arable land	Non-irrigated arable land

	Agricultural areas		Permanently irrigated land
			Rice fields
		Permanent crops	Vineyards
			Fruit trees and berry plantations
			Olive groves
		Pastures	Pastures
		Heterogeneous agricultural areas	Annual crops associated with permanent crops
			Complex cultivation patterns
			Land principally occupied by agriculture, with significant areas of natural vegetation
			Agro-forestry areas
Forest	Forest and semi natural areas	Forests	Broad-leaved forest
			Coniferous forest
			Mixed forest
Semi-natural	Forest and semi natural areas	Scrub and/or herbaceous vegetation associations	Natural grasslands
			Moors and heathland

			Sclerophyllous vegetation
			Transitional woodland-shrub
		Open spaces with little or no vegetation	Beaches, dunes, sands
			Bare rocks
			Sparsely vegetated areas
			Burnt areas
			Glaciers and perpetual snow
Wetland	Wetlands	Inland wetlands	Inland marshes
			Peat bogs
		Maritime wetlands	Salt marshes
			Salines
			Intertidal flats
	Water bodies	Inland waters	Water courses
			Water bodies

Table A.3.3. Resources (with code) used for the resource requirements matrix.

Resource	Resource categories	Resource sub-categories with code
Summer diet		Below-ground invertebrates (SIB)
		Above-ground invertebrates (SIA)
		Plant material (SPF)
		Seeds (SS)
		Vertebrates (SV)
Winter diet		Below-ground invertebrates (WIB)
		Above-ground invertebrates (WIA)
		Plant material (WPF)
		Seeds (WS)
		Vertebrates (WV)
Foraging habitat	Forest habitat preference	Deciduous (DF)
		Coniferous (CF)
	Horizontal habitat	Edge (ED)
		Core (CO)
	Vertical habitat	Ground (GR)
		Shrub (SH)
		Canopy (CA)

		Deadwood (DE)
Nest type		Hole - dead wood (NHD)
		Hole - live wood (NHL)
		Scrub/canopy (NSCA)
		Ground (NGR)
Nesting habitat	Forest habitat preference	Deciduous (DF)
		Coniferous (CF)
	Horizontal habitat	Edge (ED)
		Core (CO)
	Vertical habitat	Ground (GR)
		Shrub (SH)
		Canopy (CA)
		Deadwood (DE)

Table A.3.4. Resource requirements matrix for 105 European Common Bird Monitoring Scheme species which are noted in the literature as using forest habitat for nesting and foraging. As per Table A.3., all plausible combinations of foraging habitat and dietary resources (summer and winter), as well as nesting habitat and nest types were identified (124 combinations for resident species, 70 combinations for migratory species).

Species	**DF**	**CF**	**ED**	**CO**	**GR**	**SH**	**CA**	**DE**	**BIB**	**BIA**	**BPF**	**BS**	**BV**	**YIB**	**YIA**	**YPF**	**YS**	**YV**	**NHD**	**NHL**	**NSCA**	**NGR**
Accipiter nisus	1	1	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0
Buteo buteo	1	1	1	1	1	0	0	0	0	0	0	0	1	1	1	0	0	1	0	0	1	0
Falco tinnunculus	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	1	0
Bonasa bonasia	1	1	1	0	1	1	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	1
Tetrao tetrix	1	1	1	0	1	1	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1
Tringa nebularia	0	1	1	0	1	0	0	0	1	1	0	0	1	1	1	0	0	1	0	0	0	1
Tringa ochropus	1	1	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0
Tringa glareola	0	1	1	1	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	1
Columba oenas	1	1	1	0	1	1	1	0	0	0	1	1	0	0	0	1	1	0	1	1	0	0
Columba palumbus	1	1	1	1	1	1	1	0	0	0	1	1	0	0	0	1	1	0	0	0	1	0
Streptopelia decaocto	1	1	1	0	1	1	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	0
Streptopelia turtur	1	0	1	0	1	0	0	0	0	0	1	1	0	0	0	1	1	0	0	0	1	0
Clamator glandarius	1	0	1	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0
Cuculus canorus	1	1	1	0	1	1	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	0
Merops apiaster	1	1	1	0	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0
Upupa epops	1	0	1	0	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	1	0	0

Jynx torquilla	1	0	1	0	1	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	0	0
Picus canus	1	0	1	0	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	1	0	0
Picus viridis	0	1	1	0	1	0	0	0	1	1	0	0	0	1	1	0	0	0	1	1	0	0
Dryocopus martius	1	1	1	1	1	1	1	1	1	1	0	0	0	1	1	0	0	0	1	1	0	0
Dendrocopos major	1	1	1	1	0	0	1	1	0	1	0	0	0	0	1	0	1	0	1	1	0	0
Dendrocopos syriacus	1	0	1	1	0	0	1	0	0	1	1	1	0	0	1	1	1	0	0	1	0	0
Dendrocopos medius	1	0	1	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0
Dendrocopos minor	1	0	1	0	0	1	1	1	0	1	0	0	0	0	1	0	0	0	1	1	0	0
Lullula arborea	1	1	1	0	1	1	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	1
Anthus trivialis	1	1	1	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1
Bombycilla garrulus	0	1	1	1	1	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0
Troglodytes troglodytes	1	1	1	1	1	1	0	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0
Prunella modularis	1	1	1	0	1	1	0	0	1	1	0	0	0	1	1	0	1	0	0	0	1	0
Erithacus rubecula	1	1	1	1	1	1	0	0	0	1	0	0	0	0	1	1	1	0	1	1	0	0
Luscinia luscinia	1	0	1	0	1	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1
Luscinia megarhynchos	1	0	1	0	1	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	0	1
Luscinia svecica	1	1	1	0	1	0	0	0	0	1	0	0	0	0	1	1	1	0	0	0	0	1
Phoenicurus phoenicurus	1	0	1	0	1	1	1	0	0	1	0	0	0	0	1	0	0	0	1	1	0	0
Saxicola rubetra	0	1	1	0	1	1	0	0	0	1	0	0	0	0	1	0	1	0	0	0	1	0
Saxicola torquatus	0	1	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0
Oenanthe hispanica	1	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0

Turdus torquatus	0	1	1	0	1	1	1	0	1	1	0	0	0	1	1	1	0	0	0	0	0	1
Turdus merula	1	1	1	1	1	1	1	0	1	1	0	0	0	1	1	1	0	0	0	0	1	0
Turdus pilaris	1	1	1	1	1	1	1	0	1	1	0	0	0	1	1	1	0	0	0	0	1	0
Turdus philomelos	1	1	1	1	1	1	0	0	1	1	0	0	0	1	1	1	0	0	0	0	1	0
Turdus iliacus	1	1	1	1	1	1	1	0	1	1	0	0	0	1	1	1	0	0	0	0	0	1
Turdus viscivorus	1	1	1	0	1	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0
Locustella naevia	1	1	1	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0
Locustella fluviatilis	1	0	1	1	1	0	0	0	1	1	0	0	0	1	1	0	0	0	0	0	0	1
Acrocephalus palustris	1	0	1	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0
Hippolais icterina	1	0	1	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0
Hippolais polyglotta	1	0	1	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0
Sylvia undata	0	1	1	0	0	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0
Sylvia cantillans	1	0	1	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0
Sylvia hortensis	1	0	1	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0
Sylvia curruca	1	1	1	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0
Sylvia communis	1	0	1	0	0	1	0	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0
Sylvia borin	1	0	1	0	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0
Sylvia atricapilla	1	0	1	1	0	1	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0
Phylloscopus bonelli	1	1	1	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1
Phylloscopus sibilatrix	1	1	1	1	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1
Phylloscopus collybita	1	1	1	1	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1

Phylloscopus trochilus	1	1	1	0	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	0	1
Regulus regulus	0	1	1	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0
Regulus ignicapillus	1	1	1	1	0	0	1	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0
Muscicapa striata	1	1	1	1	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0
Ficedula albicollis	1	0	1	1	1	1	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0
Ficedula hypoleuca	1	1	1	1	1	1	1	0	0	1	0	0	0	0	1	1	0	0	1	1	0	0
Aegithalos caudatus	1	0	1	1	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0
Poecile palustris	1	0	1	1	1	1	1	0	0	1	0	0	0	0	1	1	1	0	1	1	0	0
Poecile montanus	1	1	1	1	0	1	1	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0
Lophophanes cristatus	1	1	1	1	1	1	1	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0
Periparus ater	0	1	1	1	0	1	1	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0
Cyanistes caeruleus	1	0	1	1	0	1	1	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0
Parus major	1	1	1	0	1	1	1	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0
Sitta europaea	1	1	0	1	1	1	1	1	0	1	0	0	0	0	1	0	1	0	1	1	0	0
Certhia familiaris	1	1	1	1	0	1	1	0	0	1	0	0	0	0	1	0	1	0	1	1	0	0
Certhia brachydactyla	1	1	1	1	0	1	1	0	0	1	0	0	0	0	1	0	0	0	0	1	0	0
Oriolus oriolus	1	0	1	0	0	0	1	0	0	1	0	0	0	0	1	1	0	0	0	0	1	0
Lanius collurio	1	1	1	0	1	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0
Lanius senator	1	0	1	0	1	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	1	0
Garrulus glandarius	1	1	1	1	1	1	1	0	1	1	1	1	0	1	1	1	1	0	0	0	1	0
Cyanopica cyana	1	1	1	0	1	0	0	0	1	1	1	1	0	1	1	1	1	0	0	0	1	0

Pica pica	1	1	1	0	1	0	0	0	1	1	1	1	0	1	1	1	1	0	0	0	1	0
Nucifraga caryocatactes	0	1	1	1	0	0	1	0	0	1	0	1	0	0	1	1	1	0	0	0	1	0
Corvus monedula	1	1	1	0	1	0	0	0	0	1	1	1	0	0	1	1	1	0	1	0	0	0
Corvus frugilegus	1	1	1	0	1	0	0	0	1	1	0	1	0	1	1	0	1	0	0	0	1	0
Corvus corone	1	1	1	0	1	1	0	0	1	1	0	1	0	1	1	0	1	0	0	0	1	0
Corvus corax	1	1	1	0	1	0	0	0	1	1	1	1	0	1	1	1	1	0	0	0	1	0
Sturnus vulgaris	1	0	1	0	1	0	0	0	1	1	0	0	0	1	1	1	1	0	0	1	0	0
Passer domesticus	1	1	1	0	1	1	0	0	0	0	0	1	0	0	1	0	1	0	0	1	0	0
Passer montanus	1	0	1	0	1	1	0	0	0	1	0	1	0	0	1	0	1	0	0	1	0	0
Fringilla coelebs	1	1	1	1	1	1	1	0	0	1	0	1	0	0	1	0	1	0	0	0	1	0
Fringilla montifringilla	1	1	1	0	1	1	1	0	0	1	1	1	0	0	1	1	1	0	0	0	1	0
Serinus serinus	0	1	1	0	1	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0
Serinus citrinella	0	1	1	0	1	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0
Carduelis chloris	1	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0
Carduelis carduelis	1	0	1	1	1	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0
Carduelis spinus	1	1	1	1	1	1	1	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0
Carduelis cannabina	1	1	1	0	1	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	1	0
Carduelis flammea	1	1	1	0	1	1	1	0	0	1	0	1	0	0	1	0	1	0	0	0	1	0
Carpodacus erythrinus	1	1	1	0	1	1	1	0	0	0	1	1	0	0	0	1	1	0	0	0	1	0
Pyrrhula pyrrhula	1	1	1	1	0	1	1	0	0	0	1	1	0	0	0	1	1	0	0	0	1	0
Coccothraustes coccothraustes	1	0	1	0	1	1	0	0	0	0	1	1	0	0	1	1	1	0	0	0	1	0

Emberiza citrinella	1	1	1	0	1	0	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	1
Emberiza cia	1	1	1	0	1	1	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	1
Emberiza hortulana	0	1	1	1	1	1	1	0	0	1	0	0	0	0	1	0	1	0	0	0	0	1
Emberiza rustica	1	1	1	1	1	1	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	1
Emberiza schoeniclus	1	1	1	0	1	1	0	0	0	1	0	1	0	0	1	0	1	0	0	0	0	1

Table A.3.5. Three-letter codes for 18 European countries for which indicator sets were produced.

Country	Three letter code
Austria	AUT
Belgium	BEL
Bulgaria	BGR
Czech Republic	CZE
Denmark	DNK
Estonia	EST
Finland	FIN
France	FRA
Germany	DEU
Ireland	IRL
Netherlands	NLD
Norway	NOR
Poland	POL
Romania	ROU
Spain	ESP
Sweden	SWE
Switzerland	CHE
United Kingdom	GBR

Table A.3.6. 62 common European breeding bird species that occur across European, regional or national level indicator sets.

Species	Full scientific name	Common name
A. caudatus	*Aegithalos caudatus*	Long-tailed Tit
A. nisus	*Accipiter nisus*	Sparrowhawk
A. trivialis	*Anthus trivialis*	Tree Pipit
B. bonasia	*Bonasia bonasia*	Hazel grouse
B. buteo	*Buteo buteo*	Buzzard
B. garrulous	*Bombycilla garrulus*	Waxwing
C. brachydactyla	*Certhia brachydactyla*	Short toed Treecreeper
C. caeruleus	*Cyanistes caeruleus*	Blue Tit
C. canorus	*Cuculus canorus*	Cuckoo
C. coccothraustes	*Coccothraustes coccothraustes*	Hawfinch
C. corax	*Corvus corax*	Raven
C. cyanus	*Cyanopica cyanus*	Azure-winged magpie
C. familiaris	*Certhia familiaris*	Treecreeper
C. flammea	*Carduelis flammea*	Redpoll

C. oenas	*Columba oenas*	Stock dove
C. palumbus	*Columba palumbus*	Woodpigeon
C. spinus	*Carduelis spinus*	Siskin
D. major	*Dendrocopos major*	Great Spotted Woodpecker
D. martius	*Dryocopus martius*	Black Woodpecker
D. medius	*Dendrocopos medius*	Middle Spotted Woodpecker
D. minor	*Dendrocopos minor*	Lesser Spotted Woodpecker
E. citrinella	*Emberiza citrinella*	Yellowhammer
E. rubecula	*Erithacus rubecula*	Robin
E. rustica	*Emberiza rustica*	Rustic bunting
F. albicollis	*Ficedula albicollis*	Collared Flycatcher
F. coelebs	*Fringilla coelebs*	Chaffinch
F. hypoleuca	*Ficedula hypoleuca*	Pied flycatcher
G. glandarius	*Garrulus glandarius*	Jay
J. torquilla	*Jynx torquilla*	Wryneck
L. arborea	*Lullula arborea*	Wood Lark
L. collurio	*Lanius collurio*	Red-backed Shrike
L. megarhynchos	*Luscinia megarhynchos*	Nightingale
M. striata	*Muscicapa striata*	Spotted Flycatcher
N. caryocatactes	*Nucifraga caryocatactes*	Spotted Nutcracker
O. oriolus	*Oriolus oriolus*	Golden Oriole
P. ater	*Periparus ater*	Coal Tit
P. bonelli	*Phylloscopus bonelli*	Bonelli's Warbler
P. canus	*Picus canus*	Grey faced Woodpecker
P. collybita	*Phylloscopus collybita*	Chiffchaff
L. cristatus	*Lophophanes cristatus*	Crested tit
P. major	*Parus major*	Great Tit
P. modularis	*Prunella modularis*	Dunnock
Pa. montanus	*Passer montanus*	Tree Sparrow
Po. montanus	*Poecile montanus*	Willow Tit
P. palustris	*Poecile palustris*	Marsh Tit
P. phoenicurus	*Phoenicurus phoenicurus*	Redstart
P. pyrrhula	*Pyrrhula pyrrhula*	Bullfinch
P. sibilatrix	*Phylloscopus sibilatrix*	Wood Warbler
P. trochilus	*Phylloscopus trochilus*	Willow Warbler
P. viridis	*Picus viridis*	Green Woodpecker
R. ignicapillus	*Regulus ignicapillus*	Firecrest
R. regulus	*Regulus regulus*	Goldcrest
S. atricapilla	*Sylvia atricapilla*	Blackcap
S. borin	*Sylvia borin*	Garden Warbler
S. cantillans	*Sylvia cantillans*	Subalpine Warbler

S. citrinella	*Serinus citrinella*	Citril Finch
S. curruca	*Sylvia curruca*	Lesser Whitethroat
S. europaea	*Sitta europaea*	Nuthatch
S. hortensis	*Sylvia hortensis*	Orphean Warbler
S. turtur	*Streptopelia turtur*	Turtle dove
S. vulgaris	*Sturnus vulgaris*	Starling
T. merula	*Turdus merula*	Blackbird
T. nebularia	*Tringa nebularia*	Greenshank
T. ochropus	*Tringa ochropus*	Green Sandpiper
T. philomelos	*Turdus philomelos*	Song Thrush
T. tetrix	*Tetrao tetrix*	Black Grouse
T. torquatus	*Turdus torquatus*	Ring Ouzel
T. troglodytes	*Troglodytes troglodytes*	Wren
T. viscivorus	*Turdus viscivorus*	Mistle Thrush

Table A.3.7. Species lists for forest bird indicators produced using the niche-based framework for the European level, for each of the five PECBMS region and for each of the 18 countries with the corresponding top-down and/or bottom-up indicators.

European	***regional - European***	***national - European***
Accipiter nisus	Accipiter nisus	Accipiter nisus
Anthus trivialis	Anthus trivialis	Anthus trivialis
Buteo buteo	Buteo buteo	Buteo buteo
Carduelis spinus	Coccothraustes coccothraustes	Carduelis spinus
Coccothraustes coccothraustes	Cuculus canorus	Coccothraustes coccothraustes
Cuculus canorus	Dendrocopos medius	Cuculus canorus
Dendrocopos medius	Dendrocopos minor	Dendrocopos medius
Dendrocopos minor	Garrulus glandarius	Dendrocopos minor
Garrulus glandarius	Luscinia megarhynchos	Garrulus glandarius
Muscicapa striata	Muscicapa striata	Luscinia megarhynchos
Oriolus oriolus	Oriolus oriolus	Muscicapa striata
Periparus ater	Periparus ater	Oriolus oriolus
Phoenicurus phoenicurus	Phoenicurus phoenicurus	Periparus ater
Phylloscopus sibilatrix	Phylloscopus sibilatrix	Phoenicurus phoenicurus
Phylloscopus trochilus	Phylloscopus trochilus	Phylloscopus sibilatrix
Picus canus	Picus canus	Phylloscopus trochilus
Picus viridis	Picus viridis	Picus canus
Regulus ignicapillus	Regulus ignicapillus	Picus viridis
Regulus regulus	Regulus regulus	Regulus ignicapillus
Serinus citrinella	Sitta europaea	Regulus regulus
Sitta europaea	Streptopelia turtur	Serinus citrinella
Streptopelia turtur	Sylvia borin	Sitta europaea
Sylvia borin	Sylvia cantillans	Streptopelia turtur
Sylvia cantillans	Tringa ochropus	Sylvia borin
Tringa nebularia		Sylvia cantillans
Tringa ochropus		Tringa nebularia
		Tringa ochropus

North			**South**		
European - regional	***regional***	***national - regional***	***European - regional***	***regional***	***national - regional***
Accipiter nisus	Accipiter nisus	Aegithalos caudatus	Accipiter nisus	Accipiter nisus	Accipiter nisus
Anthus trivialis	Aegithalos caudatus	Anthus trivialis	Anthus trivialis	Aegithalos caudatus	Aegithalos caudatus
Buteo buteo	Anthus trivialis	Cuculus canorus	Buteo buteo	Anthus trivialis	Anthus trivialis
Carduelis spinus	Cuculus canorus	Dendrocopos major	Carduelis spinus	Coccothraustes coccothraustes	Coccothraustes coccothraustes
Coccothraustes coccothraustes	Dendrocopos major	Garrulus glandarius	Coccothraustes coccothraustes	Cuculus canorus	Cuculus canorus
Cuculus canorus	Garrulus glandarius	Lanius collurio	Cuculus canorus	Dendrocopos medius	Dendrocopos medius
Garrulus glandarius	Muscicapa striata	Muscicapa striata	Dendrocopos medius	Dendrocopos minor	Dendrocopos minor
Muscicapa striata	Periparus ater	Periparus ater	Dendrocopos minor	Garrulus glandarius	Garrulus glandarius
Periparus ater	Phoenicurus phoenicurus	Phoenicurus phoenicurus	Garrulus glandarius	Periparus ater	Jynx torquilla
Phoenicurus phoenicurus	Phylloscopus collybita	Phylloscopus collybita	Muscicapa striata	Phoenicurus phoenicurus	Periparus ater
Phylloscopus sibilatrix	Phylloscopus trochilus	Phylloscopus trochilus	Oriolus oriolus	Phylloscopus bonelli	Phoenicurus phoenicurus
Phylloscopus trochilus	Prunella modularis	Prunella modularis	Periparus ater	Phylloscopus sibilatrix	Phylloscopus bonelli
Picus viridis	Regulus regulus	Regulus regulus	Phoenicurus phoenicurus	Phylloscopus trochilus	Phylloscopus sibilatrix
Regulus regulus	Sylvia curruca	Sylvia borin	Phylloscopus sibilatrix	Regulus ignicapillus	Phylloscopus trochilus
Sitta europaea	Tringa ochropus	Sylvia curruca	Phylloscopus trochilus	Regulus regulus	Regulus ignicapillus
Sylvia borin	Turdus viscivorus	Tringa nebularia	Picus viridis	Sitta europaea	Regulus regulus
Tringa nebularia		Tringa ochropus	Regulus ignicapillus	Sylvia borin	Sitta europaea
Tringa ochropus		Turdus viscivorus	Regulus regulus	Sylvia cantillans	Sylvia borin
			Sitta europaea		Sylvia cantillans
			Streptopelia turtur		
			Sylvia borin		
			Sylvia cantillans		

Central & East			West		
European - regional	***regional***	***national - regional***	***European - regional***	***regional***	***national - regional***
Accipiter nisus	Accipiter nisus	Accipiter nisus	Accipiter nisus	Accipiter nisus	Accipiter nisus
Anthus trivialis	Anthus trivialis	Aegithalos caudatus	Anthus trivialis	Anthus trivialis	Anthus trivialis
Buteo buteo	Coccothraustes coccothraustes	Anthus trivialis	Buteo buteo	Buteo buteo	Buteo buteo
Carduelis spinus	Dendrocopos major	Buteo buteo	Carduelis spinus	Coccothraustes coccothraustes	Coccothraustes coccothraustes
Coccothraustes coccothraustes	Dendrocopos medius	Coccothraustes coccothraustes	Coccothraustes coccothraustes	Dendrocopos medius	Dendrocopos medius
Cuculus canorus	Dendrocopos minor	Dendrocopos major	Cuculus canorus	Dendrocopos minor	Dendrocopos minor
Dendrocopos medius	Garrulus glandarius	Dendrocopos medius	Dendrocopos medius	Garrulus glandarius	Garrulus glandarius
Dendrocopos minor	Nucifraga caryocatactes	Dendrocopos minor	Dendrocopos minor	Jynx torquilla	Lullula arborea
Garrulus glandarius	Oriolus oriolus	Garrulus glandarius	Garrulus glandarius	Lullula arborea	Luscinia megarhynchos
Muscicapa striata	Periparus ater	Oriolus oriolus	Muscicapa striata	Oriolus oriolus	Oriolus oriolus
Oriolus oriolus	Phylloscopus sibilatrix	Periparus ater	Oriolus oriolus	Periparus ater	Periparus ater
Periparus ater	Phylloscopus trochilus	Phoenicurus phoenicurus	Periparus ater	Phoenicurus phoenicurus	Phoenicurus phoenicurus
Phoenicurus phoenicurus	Picus canus	Phylloscopus sibilatrix	Phoenicurus phoenicurus	Phylloscopus sibilatrix	Phylloscopus sibilatrix
Phylloscopus sibilatrix	Regulus ignicapillus	Phylloscopus trochilus	Phylloscopus sibilatrix	Picus canus	Picus canus
Phylloscopus trochilus	Regulus regulus	Picus canus	Phylloscopus trochilus	Picus viridis	Picus viridis
Picus canus	Streptopelia turtur	Regulus ignicapillus	Picus canus	Regulus ignicapillus	Regulus ignicapillus
Picus viridis	Sylvia borin	Regulus regulus	Picus viridis	Regulus regulus	Regulus regulus
Regulus ignicapillus	Tringa ochropus	Streptopelia turtur	Regulus ignicapillus	Sitta europaea	Sitta europaea
Regulus regulus		Sylvia borin	Regulus regulus	Streptopelia turtur	Streptopelia turtur
Sitta europaea		Tringa ochropus	Serinus citrinella	Sylvia atricapilla	Sylvia atricapilla
Streptopelia turtur		Troglodytes troglodytes	Sitta europaea	Sylvia borin	Sylvia borin
Sylvia borin		Turdus viscivorus	Streptopelia turtur	Turdus torquatus	Turdus torquatus
Tringa ochropus			Sylvia borin		

Southeast		
European - regional	***regional***	***national - regional***
Anthus trivialis	Anthus trivialis	Cuculus canorus
Buteo buteo	Buteo buteo	Dendrocopos major
Coccothraustes coccothraustes	Coccothraustes coccothraustes	Garrulus glandarius
Cuculus canorus	Cuculus canorus	Oriolus oriolus
Garrulus glandarius	Cyanistes caeruleus	Parus major
Oriolus oriolus	Dendrocopos major	Phylloscopus collybita
Sitta europaea	Emberiza citrinella	Sturnus vulgaris
Streptopelia turtur	Erithacus rubecula	Sylvia atricapilla
	Garrulus glandarius	
	Luscinia megarhynchos	
	Oriolus oriolus	
	Phylloscopus collybita	
	Sitta europaea	
	Streptopelia turtur	
	Sylvia atricapilla	

North								
Finland			**Norway**			**Sweden**		
European - national	***regional - national***	***national***	***European - national***	***regional - national***	***national***	***European - national***	***regional - national***	***national***
Anthus trivialis	Anthus trivialis	Anthus trivialis	Anthus trivialis	Anthus trivialis	Anthus trivialis	Anthus trivialis	Aegithalos caudatus	Aegithalos caudatus
Carduelis spinus	Cuculus canorus	Cuculus canorus	Carduelis spinus	Cuculus canorus	Columba palumbus	Buteo buteo	Anthus trivialis	Anthus trivialis
Cuculus canorus	Dendrocopos major	Dryocopus martius	Cuculus canorus	Dendrocopos major	Dendrocopos major	Carduelis spinus	Cuculus canorus	Bombycilla garrulus
Garrulus glandarius	Garrulus glandarius	Garrulus glandarius	Muscicapa striata	Muscicapa striata	Muscicapa striata	Coccothraustes coccothraustes	Dendrocopos major	Cuculus canorus
Muscicapa striata	Muscicapa striata	Lanius collurio	Periparus ater	Periparus ater	Periparus ater	Cuculus canorus	Garrulus glandarius	Dendrocopos major
Periparus ater	Periparus ater	Muscicapa striata	Phoenicurus phoenicurus	Phoenicurus phoenicurus	Phoenicurus phoenicurus	Garrulus glandarius	Muscicapa striata	Garrulus glandarius
Phoenicurus phoenicurus	Phoenicurus phoenicurus	Phoenicurus phoenicurus	Phylloscopus trochilus	Phylloscopus collybita	Phylloscopus collybita	Muscicapa striata	Periparus ater	Muscicapa striata
Phylloscopus sibilatrix	Phylloscopus collybita	Phylloscopus collybita	Regulus regulus	Phylloscopus trochilus	Phylloscopus trochilus	Periparus ater	Phoenicurus phoenicurus	Periparus ater
Phylloscopus trochilus	Phylloscopus trochilus	Phylloscopus trochilus	Sylvia borin	Prunella modularis	Prunella modularis	Phoenicurus phoenicurus	Phylloscopus collybita	Phoenicurus phoenicurus
Regulus regulus	Prunella modularis	Prunella modularis	Tringa nebularia	Regulus regulus	Regulus regulus	Phylloscopus sibilatrix	Phylloscopus trochilus	Phylloscopus collybita
Sylvia borin	Regulus regulus	Regulus regulus			Tringa nebularia	Phylloscopus trochilus	Prunella modularis	Phylloscopus trochilus
Tringa nebularia	Sylvia curruca	Sylvia borin			Turdus philomelos	Picus viridis	Regulus regulus	Prunella modularis
Tringa ochropus	Tringa ochropus	Sylvia curruca				Regulus regulus	Sylvia curruca	Regulus regulus
	Turdus viscivorus	Tringa ochropus				Sitta europaea	Tringa ochropus	Sylvia curruca
		Turdus viscivorus				Sylvia borin	Turdus viscivorus	Tetrao tetrix
						Tringa nebularia		Tringa ochropus
						Tringa ochropus		Turdus viscivorus

South					
France			**Spain**		
European - national	***regional - national***	***national***	***European - national***	***regional - national***	***national***
Anthus trivialis	Aegithalos caudatus	Anthus trivialis	Accipiter nisus	Accipiter nisus	Accipiter nisus
Buteo buteo	Anthus trivialis	Coccothraustes coccothraustes	Anthus trivialis	Aegithalos caudatus	Aegithalos caudatus
Coccothraustes coccothraustes	Coccothraustes coccothraustes	Cuculus canorus	Buteo buteo	Anthus trivialis	Anthus trivialis
Cuculus canorus	Cuculus canorus	Dendrocopos medius	Carduelis spinus	Coccothraustes coccothraustes	Certhia brachydactyla
Dendrocopos medius	Dendrocopos medius	Dendrocopos minor	Coccothraustes coccothraustes	Dendrocopos minor	Coccothraustes coccothraustes
Dendrocopos minor	Dendrocopos minor	Garrulus glandarius	Cuculus canorus	Garrulus glandarius	Cyanistes caeruleus
Garrulus glandarius	Garrulus glandarius	Jynx torquilla	Dendrocopos minor	Periparus ater	Garrulus glandarius
Muscicapa striata	Periparus ater	Periparus ater	Garrulus glandarius	Phylloscopus bonelli	Periparus ater
Oriolus oriolus	Phoenicurus phoenicurus	Phoenicurus phoenicurus	Muscicapa striata	Regulus ignicapillus	Phylloscopus bonelli
Periparus ater	Phylloscopus bonelli	Phylloscopus bonelli	Oriolus oriolus	Regulus regulus	Regulus ignicapillus
Phoenicurus phoenicurus	Phylloscopus sibilatrix	Phylloscopus sibilatrix	Periparus ater	Sitta europaea	Regulus regulus
Phylloscopus sibilatrix	Phylloscopus trochilus	Phylloscopus trochilus	Picus viridis	Sylvia borin	Sitta europaea
Phylloscopus trochilus	Regulus ignicapillus	Regulus ignicapillus	Regulus ignicapillus	Sylvia cantillans	Sylvia borin
Picus viridis	Regulus regulus	Regulus regulus	Regulus regulus		Sylvia hortensis
Regulus ignicapillus	Sitta europaea	Sitta europaea	Sitta europaea		
Regulus regulus	Sylvia borin	Sylvia borin	Streptopelia turtur		
Sitta europaea	Sylvia cantillans	Sylvia cantillans	Sylvia borin		
Streptopelia turtur			Sylvia cantillans		
Sylvia borin					
Sylvia cantillans					

Central & East											
Czech Republic			**Estonia**			**Germany**			**Poland**		
European - national	***regional - national***	***national***	***European - national***	***regional - national***	***national***	***European - national***	***regional - national***	***national***	***European - national***	***regional - national***	***national***
Anthus trivialis	Anthus trivialis	Columba palumbus	Cuculus canorus	Phylloscopus sibilatrix	Columba palumbus	Accipiter nisus	Accipiter nisus	Accipiter nisus	Accipiter nisus	Accipiter nisus	Accipiter nisus
Buteo buteo	Coccothraustes coccothraustes	Corvus corax	Phylloscopus sibilatrix	Phylloscopus trochilus	Cuculus canorus	Anthus trivialis	Anthus trivialis	Anthus trivialis	Anthus trivialis	Anthus trivialis	Aegithalos caudatus
Coccothraustes coccothraustes	Dendrocopos major	Dryocopus martius	Phylloscopus trochilus	Sylvia borin	Erithacus rubecula	Buteo buteo	Buteo buteo	Buteo buteo	Buteo buteo	Coccothraustes coccothraustes	Anthus trivialis
Cuculus canorus	Garrulus glandarius	Erithacus rubecula	Sylvia borin		Phylloscopus sibilatrix	Coccothraustes coccothraustes	Coccothraustes coccothraustes	Certhia familiaris	Carduelis spinus	Dendrocopos major	Coccothraustes coccothraustes
Garrulus glandarius	Oriolus oriolus	Ficedula albicollis			Phylloscopus trochilus	Cuculus canorus	Dendrocopos major	Coccothraustes coccothraustes	Coccothraustes coccothraustes	Dendrocopos minor	Dendrocopos major
Muscicapa striata	Periparus ater	Periparus ater			Sylvia atricapilla	Dendrocopos medius	Dendrocopos medius	Dendrocopos major	Cuculus canorus	Garrulus glandarius	Erithacus rubecula
Oriolus oriolus	Phylloscopus sibilatrix	Phylloscopus sibilatrix			Sylvia borin	Dendrocopos minor	Dendrocopos minor	Dendrocopos medius	Dendrocopos minor	Oriolus oriolus	Garrulus glandarius
Periparus ater	Phylloscopus trochilus	Prunella modularis			Turdus merula	Garrulus glandarius	Garrulus glandarius	Dendrocopos minor	Garrulus glandarius	Periparus ater	Oriolus oriolus
Phoenicurus phoenicurus	Regulus ignicapillus	Pyrrhula pyrrhula			Turdus philomelos	Muscicapa striata	Jynx torquilla	Garrulus glandarius	Muscicapa striata	Phylloscopus sibilatrix	Periparus ater
Phylloscopus sibilatrix	Regulus regulus	Regulus ignicapillus				Oriolus oriolus	Lullula arborea	Oriolus oriolus	Oriolus oriolus	Phylloscopus trochilus	Phoenicurus phoenicurus
Phylloscopus trochilus	Streptopelia turtur	Regulus regulus				Periparus ater	Oriolus oriolus	Periparus ater	Periparus ater	Regulus ignicapillus	Phylloscopus sibilatrix
Picus viridis	Sylvia borin	Sylvia atricapilla				Phoenicurus phoenicurus	Periparus ater	Phylloscopus sibilatrix	Phoenicurus phoenicurus	Regulus regulus	Phylloscopus trochilus
Regulus ignicapillus		Sylvia borin				Phylloscopus sibilatrix	Phoenicurus phoenicurus	Phylloscopus trochilus	Phylloscopus sibilatrix	Streptopelia turtur	Prunella modularis
Regulus regulus		Turdus viscivorus				Phylloscopus trochilus	Phylloscopus sibilatrix	Picus canus	Phylloscopus trochilus	Sylvia borin	Regulus ignicapillus
Sitta europaea						Picus canus	Phylloscopus trochilus	Regulus ignicapillus	Picus viridis	Tringa ochropus	Regulus regulus
Streptopelia turtur						Picus viridis	Picus canus	Regulus regulus	Regulus ignicapillus		Streptopelia turtur
Sylvia borin						Regulus ignicapillus	Picus viridis	Streptopelia turtur	Regulus regulus		Sylvia atricapilla
						Regulus regulus	Regulus ignicapillus	Turdus viscivorus	Sitta europaea		Sylvia borin
						Sitta europaea	Regulus regulus		Streptopelia turtur		Tringa ochropus
						Streptopelia turtur	Sitta europaea		Sylvia borin		Troglodytes troglodytes
						Sylvia borin	Streptopelia turtur		Tringa ochropus		Turdus viscivorus
							Sylvia atricapilla				
							Sylvia borin				

West								
Austria			**Belgium**			**Denmark**		
European - national	***regional - national***	***national***	***European - national***	***regional - national***	***national***	***European - national***	***regional - national***	***national***
Austria	**Austria**	**Austria**	**Belgium**	**Belgium**	**Belgium**	**Denmark**	**Denmark**	**Denmark**
Anthus trivialis	Anthus trivialis	Aegithalos caudatus	Anthus trivialis	Anthus trivialis	Aegithalos caudatus	Anthus trivialis	Anthus trivialis	Anthus trivialis
Buteo buteo	Buteo buteo	Certhia familiaris	Buteo buteo	Buteo buteo	Buteo buteo	Buteo buteo	Buteo buteo	Buteo buteo
Coccothraustes coccothraustes	Coccothraustes coccothraustes	Coccothraustes coccothraustes	Coccothraustes coccothraustes	Coccothraustes coccothraustes	Coccothraustes coccothraustes	Cuculus canorus	Garrulus glandarius	Certhia familiaris
Cuculus canorus	Garrulus glandarius	Dryocopus martius	Cuculus canorus	Garrulus glandarius	Cuculus canorus	Garrulus glandarius	Periparus ater	Dendrocopos major
Garrulus glandarius	Oriolus oriolus	Garrulus glandarius	Garrulus glandarius	Periparus ater	Dendrocopos major	Muscicapa striata	Phoenicurus phoenicurus	Garrulus glandarius
Muscicapa striata	Periparus ater	Periparus ater	Periparus ater	Picus viridis	Garrulus glandarius	Periparus ater	Phylloscopus sibilatrix	Muscicapa striata
Oriolus oriolus	Phoenicurus phoenicurus	Phylloscopus collybita	Phylloscopus trochilus	Regulus ignicapillus	Periparus ater	Phoenicurus phoenicurus	Regulus regulus	Periparus ater
Periparus ater	Picus viridis	Phylloscopus trochilus	Picus viridis	Regulus regulus	Phylloscopus collybita	Phylloscopus sibilatrix	Sitta europaea	Phoenicurus phoenicurus
Phoenicurus phoenicurus	Regulus ignicapillus	Regulus ignicapillus	Regulus ignicapillus	Sitta europaea	Phylloscopus trochilus	Phylloscopus trochilus	Sylvia atricapilla	Phylloscopus sibilatrix
Phylloscopus trochilus	Regulus regulus	Regulus regulus	Regulus regulus	Sylvia atricapilla	Poecile palustris	Regulus regulus	Sylvia borin	Phylloscopus trochilus
Picus viridis	Sitta europaea	Sylvia atricapilla	Sitta europaea	Sylvia borin	Regulus ignicapillus	Sitta europaea		Regulus regulus
Regulus ignicapillus	Streptopelia turtur	Troglodytes troglodytes	Sylvia borin		Regulus regulus	Sylvia borin		Sitta europaea
Regulus regulus	Sylvia atricapilla				Sitta europaea			Sylvia atricapilla
Sitta europaea	Sylvia borin				Sylvia borin			Sylvia borin
Streptopelia turtur					Turdus viscivorus			Turdus viscivorus
Sylvia borin								

West

Ireland			Netherlands			Switzerland			United Kingdom		
European - national	***regional - national***	***national***	***European - national***	***regional - national***	***national***	***European - national***	***regional - national***	***national***	***European - national***	***regional - national***	***national***
Ireland	**Ireland**	**Ireland**	**Netherlands**	**Netherlands**	**Netherlands**	**Switzerland**	**Switzerland**	**Switzerland**	**United Kingdom**	**United Kingdom**	**United Kingdom**
Cuculus canorus	Periparus ater	Corvus corax	Accipiter nisus	Accipiter nisus	Accipiter nisus	Anthus trivialis	Anthus trivialis	Aegithalos caudatus	Accipiter nisus	Accipiter nisus	Anthus trivialis
Periparus ater	Regulus regulus	Cuculus canorus	Anthus trivialis	Anthus trivialis	Aegithalos caudatus	Buteo buteo	Buteo buteo	Anthus trivialis	Anthus trivialis	Anthus trivialis	Buteo buteo
Phylloscopus trochilus	Sylvia atricapilla	Erithacus rubecula	Buteo buteo	Buteo buteo	Anthus trivialis	Carduelis spinus	Coccothraustes coccothraustes	Buteo buteo	Buteo buteo	Buteo buteo	Carduelis flammea
Regulus regulus		Fringilla coelebs	Coccothraustes coccothraustes	Coccothraustes coccothraustes	Buteo buteo	Coccothraustes coccothraustes	Garrulus glandarius	Cuculus canorus	Carduelis spinus	Garrulus glandarius	Carduelis spinus
		Periparus ater	Cuculus canorus	Dendrocopos minor	Certhia brachydactyla	Cuculus canorus	Periparus ater	Emberiza citrinella	Cuculus canorus	Periparus ater	Cuculus canorus
		Phylloscopus trochilus	Dendrocopos minor	Garrulus glandarius	Coccothraustes coccothraustes	Garrulus glandarius	Phoenicurus phoenicurus	Garrulus glandarius	Garrulus glandarius	Phoenicurus phoenicurus	Garrulus glandarius
		Regulus regulus	Garrulus glandarius	Lullula arborea	Dendrocopos major	Muscicapa striata	Phylloscopus sibilatrix	Lanius collurio	Muscicapa striata	Phylloscopus sibilatrix	Periparus ater
		Sylvia atricapilla	Muscicapa striata	Oriolus oriolus	Dendrocopos minor	Periparus ater	Picus viridis	Nucifraga caryocatactes	Periparus ater	Picus viridis	Phoenicurus phoenicurus
		Turdus philomelos	Oriolus oriolus	Periparus ater	Garrulus glandarius	Phoenicurus phoenicurus	Regulus ignicapillus	Passer montanus	Phoenicurus phoenicurus	Regulus regulus	Phylloscopus sibilatrix
		Turdus viscivorus	Periparus ater	Phoenicurus phoenicurus	Lullula arborea	Phylloscopus sibilatrix	Regulus regulus	Phoenicurus phoenicurus	Phylloscopus sibilatrix	Sitta europaea	Phylloscopus trochilus
			Phoenicurus phoenicurus	Phylloscopus sibilatrix	Luscinia megarhynchos	Picus viridis	Sitta europaea	Phylloscopus-sibilatrix	Phylloscopus trochilus	Streptopelia turtur	Picus viridis
			Phylloscopus sibilatrix	Picus viridis	Oriolus oriolus	Regulus ignicapillus	Sylvia atricapilla	Picus viridis	Picus viridis	Sylvia atricapilla	Poecile palustris
			Phylloscopus trochilus	Regulus regulus	Periparus ater	Regulus regulus	Sylvia borin	Regulus ignicapillus	Regulus regulus	Sylvia borin	Regulus regulus
			Picus viridis	Sitta europaea	Phoenicurus phoenicurus	Serinus citrinella	Turdus torquatus	Regulus regulus	Sitta europaea		Sitta europaea
			Regulus regulus	Streptopelia turtur	Phylloscopus sibilatrix	Sitta europaea		Serinus citrinella	Streptopelia turtur		Streptopelia turtur
			Sitta europaea	Sylvia atricapilla	Picus viridis	Sylvia borin		Sitta europaea	Sylvia borin		Sylvia borin
			Streptopelia turtur	Sylvia borin	Regulus regulus			Sylvia atricapilla			
			Sylvia borin		Streptopelia turtur			Sylvia borin			
					Sylvia borin			Turdus torquatus			

Southeast

Bulgaria			Romania		
European - national	***regional - national***	***national***	***European - national***	***regional - national***	***national***
Cuculus canorus	Cuculus canorus	Cuculus canorus	Anthus trivialis	Anthus trivialis	Cuculus canorus
Garrulus glandarius	Garrulus glandarius	Fringilla coelebs	Cuculus canorus	Cuculus canorus	Dendrocopos major
		Garrulus glandarius	Garrulus glandarius	Dendrocopos major	Garrulus glandarius
		Parus major	Oriolus oriolus	Emberiza citrinella	Oriolus oriolus
				Erithacus rubecula	Phylloscopus collybita
				Garrulus glandarius	Sturnus vulgaris
				Oriolus oriolus	Sylvia atricapilla
				Phylloscopus collybita	
				Sylvia atricapilla	

Table A.3.8. Overall percentage change, standard error (SE) of percentage change, description of overall trend and significance of that trend for MSIs for forest habitat generated for *European, regional* and *national* indicators with their corresponding top-down (*European - regional, European - national, regional - national*) and/or bottom-up (*national - regional, national - European, regional - European*) approach to indicator species selection. Set size of each indicator provided in brackets. Significant trends are highlighted in bold.

Spatial scale	**Indicator Set (Set Size)**	**% change**	**SE % change**	**Trend**	**Significance**
Europe	*European* (26)	4.391	6.574	stable	n.s.
	regional - European (24)	5.698	7.091	stable	n.s.
	national - European (27)	4.827	6.42	stable	n.s.
North	*European - regional* (18)	1.458	5.615	stable	n.s.
	regional (16)	12.755	7.763	stable	n.s.
	national - regional (18)	10.504	5.869	stable	n.s.
South	*European - regional* (22)	12.687	14.311	stable	n.s.
	regional (18)	18.957	15.772	stable	n.s.
	national - regional (19)	13.515	15.247	stable	n.s.
Central & East	*European - regional* (23)	5.731	8.65	stable	n.s.
	regional (18)	9.556	11.746	stable	n.s.
	national - regional (22)	10.281	8.85	stable	n.s.
West	*European - regional* (23)	-10.611	5.251	moderate decline	**p<0.05**
	regional (22)	-4.393	5.96	stable	n.s.
	national - regional (22)	-4.651	5.395	stable	n.s.
Southeast	*European - regional* (8)	-13.381	8.722	stable	n.s.
	regional (15)	17.514	8.011	moderate increase	**p<0.05**
	national - regional (8)	11.315	7.658	moderate increase	n.s.
Finland	*European - national* (13)	-11.477	3.529	moderate decline	**p<0.01**
	regional - national (14)	15.514	4.589	moderate increase	**p<0.01**
	national (15)	12.307	4.311	moderate increase	**p<0.01**
Norway	*European - national* (10)	-12.064	3.135	moderate decline	**p<0.01**
	regional - national (10)	-6.081	3.122	moderate decline	n.s.
	national (12)	-1.935	3.036	stable	n.s.
Sweden	*European - national* (17)	30.401	4.566	moderate increase	**p<0.01**
	regional - national (15)	43.456	4.741	moderate increase	**p<0.01**
	national (17)	60.256	7.831	moderate increase	**p<0.01**
France	*European - national* (20)	16.033	6.668	stable	**p<0.05**
	regional - national (17)	25.843	8.192	moderate increase	**p<0.01**
	national (17)	23.285	8.229	moderate increase	**p<0.01**
Spain	*European - national* (18)	34.207	18.432	moderate increase	n.s.

	regional - national (14)	49.707	24.72	moderate increase	n.s.
	national (14)	29.877	17.241	moderate increase	n.s.
Czech Republic	*European - national* (17)	-12.102	3.266	moderate decline	**p<0.01**
	regional - national (12)	-14.013	3.4	moderate decline	**p<0.01**
	national (14)	17.244	6.107	moderate increase	**p<0.01**
Estonia	*European - national* (4)	-29.954	5.148	moderate decline	**p<0.01**
	regional - national (3)	-42.224	4.636	moderate decline	**p<0.01**
	national (9)	-12.125	4.686	stable	**p<0.01**
Poland	*European - national* (21)	40.058	18.963	moderate increase	**p<0.05**
	regional - national (15)	23.885	15.608	stable	n.s.
	national (21)	27.927	10.681	moderate increase	**p<0.01**
Germany*	*European - national* (21)	-2.501	3.245	stable	n.s.
	regional - national (23)	3.679	3.448	stable	n.s.
	national (18)	4.227	3.964	stable	n.s.
Austria	*European - national* (16)	-24.255	2.487	moderate decline	**p<0.01**
	regional - national (14)	-19.892	2.622	moderate decline	**p<0.01**
	national (12)	-20.431	3.082	moderate decline	**p<0.01**
Belgium	*European - national* (12)	-17.592	3.122	moderate decline	**p<0.01**
	regional - national (11)	-8.025	3.56	moderate decline	**p<0.05**
	national (15)	-16.976	3.029	moderate decline	**p<0.01**
Denmark	*European - national* (12)	-23.501	3.323	moderate decline	**p<0.01**
	regional - national (10)	-9.194	3.963	stable	**p<0.05**
	national (15)	-12.989	3.676	moderate decline	**p<0.01**
Ireland	*European - national* (4)	22.852	7.081	moderate increase	**p<0.01**
	regional - national (3)	145.263	19.72	moderate increase	**p<0.01**
	national (10)	50.899	6.053	moderate increase	**p<0.01**
Netherlands	*European - national* (18)	-29.79	3.01	moderate decline	**p<0.01**
	regional - national (17)	-23.872	3.493	moderate decline	**p<0.01**
	national (19)	-24.618	3.146	moderate decline	**p<0.01**
Switzerland	*European - national* (16)	1.269	4.179	stable	n.s.
	regional - national (14)	-1.653	3.388	stable	n.s.
	national (19)	-0.417	2.946	stable	n.s.
United Kingdom	*European - national* (16)	-24.76	1.354	moderate decline	**p<0.01**
	regional - national (13)	-17.002	1.634	moderate decline	**p<0.01**
	national (16)	-22.115	1.472	moderate decline	**p<0.01**
Bulgaria	*European - national* (2)	-25.144	12.206	moderate decline	**p<0.05**
	regional - national (2)	-25.242	12.185	moderate decline	**p<0.05**
	national (4)	-13.919	10.953	stable	n.s.
Romania	*European - national* (4)	8.969	13.382	stable	n.s.
	regional - national (9)	15.168	8.149	stable	n.s.
	national (7)	27.297	10.917	stable	**p<0.05**

Table A.3.9. Results for differences in long-term trends between MSIs for each spatial scale. Difference in the trends, standard error in the difference and significance of the difference in trends are shown. Significant results are highlighted in bold.

Spatial scale		***European***	***European* vs *national - European***	***Regional - European vs national - European***
Europe	trend diff.	0.001605	0.000265	-0.001029
	SE diff.	0.003671	0.003574	0.003582
	significance	n.s.	n.s.	n.s.
		European - regional vs regional	***regional vs national - regional***	***European - regional vs national - regional***
North	trend diff.	0.005418	-0.000202	-0.005687
	SE diff.	0.003192	0.003473	0.003564
	significance	n.s.	n.s.	n.s.
South	trend diff.	0.000851	-0.002229	-0.002951
	SE diff.	0.007492	0.007474	0.007706
	significance	n.s.	n.s.	n.s.
Central & East	trend diff.	0.001536	0.001885	0.000322
	SE diff.	0.004832	0.005359	0.005419
	significance	n.s.	n.s.	n.s.
West	trend diff.	0.003748	0.000335	-0.003452
	SE diff.	0.003356	0.003581	0.003458
	significance	n.s.	n.s.	n.s.
Southeast	trend diff.	0.007623	-0.007349	-0.014382
	SE diff.	0.007371	0.005967	0.007545
	significance	n.s.	n.s.	n.s.
		European - national vs national	***regional - national vs national***	***European - national vs regional - national***
Finland	trend diff.	-0.010477	0.000925	0.011353
	SE diff.	0.002087	0.002192	0.002187
	significance	**p<0.05**	n.s.	**p<0.05**
Norway	trend diff.	-0.001283	-0.003829	-0.003055
	SE diff.	0.012879	0.01035	0.013205
	significance	n.s.	n.s.	n.s.
Sweden	trend diff.	-0.009619	-0.002368	0.007249
	SE diff.	0.002475	0.002483	0.002025
	significance	**p<0.05**	n.s.	**p<0.05**
France	trend diff.	-0.003859	0.001415	0.005281
	SE diff.	0.004236	0.004714	0.004511
	significance	n.s.	n.s.	n.s.
Spain	trend diff.	-0.002106	0.005066	0.006604

	SE diff.	0.007053	0.008283	0.008662
	significance	n.s.	n.s.	n.s.
Czech Republic	trend diff.	-0.015871	-0.017058	-0.000968
	SE diff.	0.002608	0.002741	0.002136
	significance	**p<0.05**	**p<0.05**	n.s.
Estonia	trend diff.	-0.005356	-0.016145	-0.010548
	SE diff.	0.003337	0.003566	0.00398
	significance	n.s.	**p<0.05**	**p<0.05**
Germany	trend diff.	-0.002787	0.00095	0.003649
	SE diff.	0.003204	0.00312	0.002844
	significance	n.s.	n.s.	n.s.
Poland	trend diff.	0.003853	-0.003415	-0.007805
	SE diff.	0.007145	0.006768	0.008341
	significance	n.s.	n.s.	n.s.
Austria	trend diff.	0.000207	0.003068	0.002656
	SE diff.	0.001991	0.001997	0.001882
	significance	n.s.	n.s.	n.s.
Belgium	trend diff.	0.000161	0.004158	0.004071
	SE diff.	0.002125	0.002157	0.002237
	significance	n.s.	n.s.	n.s.
Denmark	trend diff.	-0.004136	0.004502	0.008595
	SE diff.	0.002026	0.002069	0.002073
	significance	**p<0.05**	**p<0.05**	**p<0.05**
Ireland	trend diff.	-0.006941	0.032337	0.039303
	SE diff.	0.002621	0.003561	0.003838
	significance	**p<0.05**	**p<0.05**	**p<0.05**
Netherlands	trend diff.	-0.003702	0.000271	0.004157
	SE diff.	0.001919	0.001916	0.002017
	significance	n.s.	n.s.	**p<0.05**
Switzerland	trend diff.	-0.000899	0.000058	0.001033
	SE diff.	0.00172	0.001487	0.001982
	significance	n.s.	n.s.	n.s.
United Kingdom	trend diff.	-0.002256	0.001734	0.00405
	SE diff.	0.001052	0.001069	0.001058
	significance	**p<0.05**	n.s.	**p<0.05**
Bulgaria	trend diff.	-0.012809	-0.012436	0.00071
	SE diff.	0.010606	0.010348	0.012478
	significance	n.s.	n.s.	n.s.
Romania	trend diff.	-0.005107	-0.00377	0.001155
	SE diff.	0.012771	0.009805	0.012317
	significance	n.s.	n.s.	n.s.

Table A.3.10. Results for differences in long-term trends between MSIs produced using the niche-based framework and the current Forest Bird Indicator for Europe, and between MSIs produced for four of the five PECBMS regions and the current Forest Bird Indicators for these same regions. PECBMS does not produce a forest bird indicator for the Southeast region so this comparison could not be made. Difference in the trends, standard error in the difference and significance of the difference in trends are shown. Significant results are highlighted in bold.

Spatial scale		**Current FoBI vs *European***	**Current FoBI vs *regional - European***	**Current FoBI vs *national - European***
Europe	trend diff.	-0.002368	-0.000653	-0.001917
	SE diff.	0.003682	0.003632	0.00347
	significance	n.s.	n.s.	n.s.
		Current FoBI vs *European - regional*	**Current FoBI vs *regional***	**Current FoBI vs *national - regional***
North	trend diff.	0.000381	0.005725	0.005655
	SE diff.	0.003329	0.003614	0.003192
	significance	n.s.	n.s.	n.s.
South	trend diff.	-0.003747	-0.000877	-0.002735
	SE diff.	0.00666	0.007118	0.007034
	significance	n.s.	n.s.	n.s.
Central & East	trend diff.	0.001112	0.000561	0.002583
	SE diff.	0.004454	0.00521	0.004417
	significance	n.s.	n.s.	n.s.
West	trend diff.	-0.009329	-0.005874	-0.005501
	SE diff.	0.003131	0.003285	0.003054
	significance	**p<0.05**	n.s.	n.s.

Table A.3.11. Percentage of scale-dependent resources covered and average sensitivity of the suite of species in the current European FoBI and regional FoBIs. Species in the current regional FoBIs are a subset of those in the European FoBI. For comparison, percentage of scale-dependent resources covered and average sensitivity of European and regional niche-based indicators are included. Set size of each indicator provided in brackets.

Spatial scale	**Indicator source**	**Percentage of scale-dependent resources**	**Average sensitivity**
Europe	Current FoBI (34)	93.55	8.053
	European (26)	100	4.870
	regional - European (24)	100	4.953
	national - European (27)	100	4.843
North	Current regional FoBI (24)	100	17.863
	European - regional (18)	100	14.038
	regional (16)	100	11.321
	national - regional (18)	86.21	11.977
South	Current regional FoBI (25)	100	9.837
	European - regional (22)	100	7.547
	regional (18)	100	6.641
	national - regional (19)	100	6.565
Central & East	Current regional FoBI (27)	100	8.77
	European - regional (23)	100	7.721
	regional (18)	100	6.433
	national - regional (22)	100	6.945
West	Current regional FoBI (29)	93.55	7.435
	European - regional (23)	100	5.144
	regional (22)	100	4.891
	national - regional (22)	100	4.901

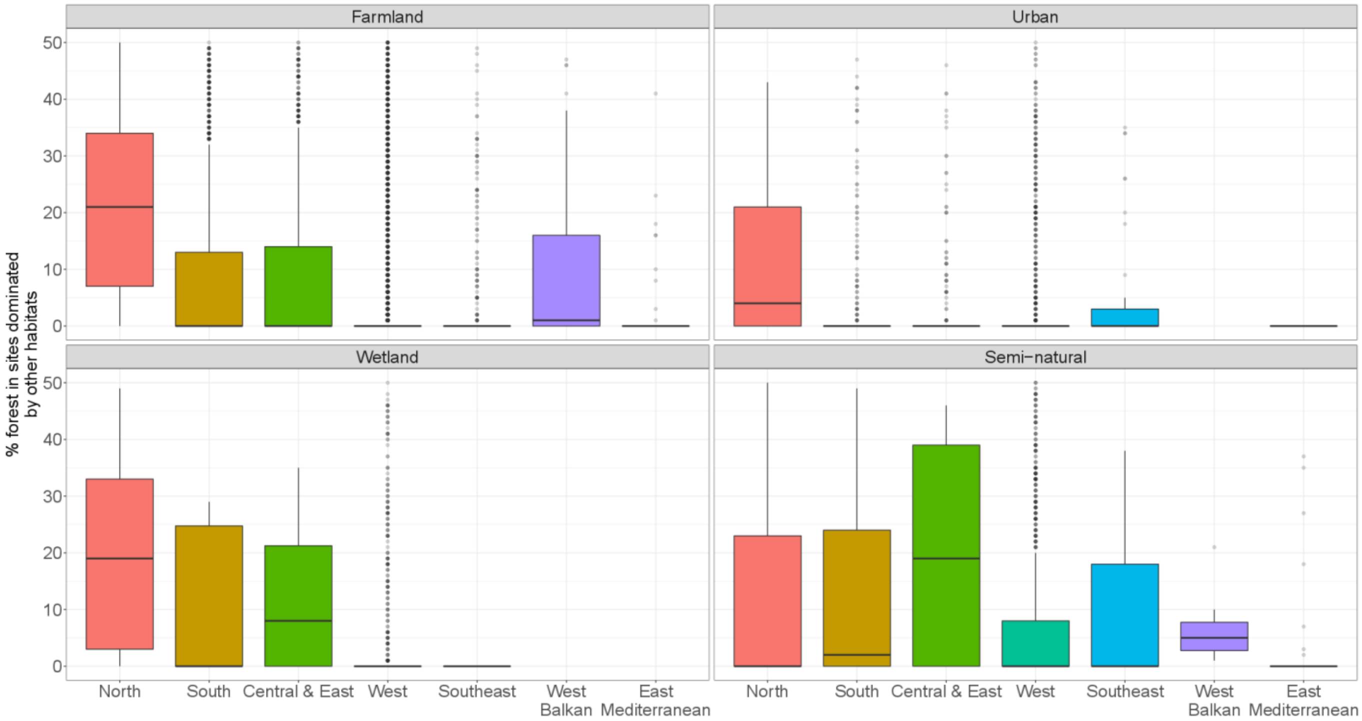


Fig. A.3.1. Proportion (as a percentage) of forest within sites dominated by farmland, urban, wetland and semi-natural habitats.

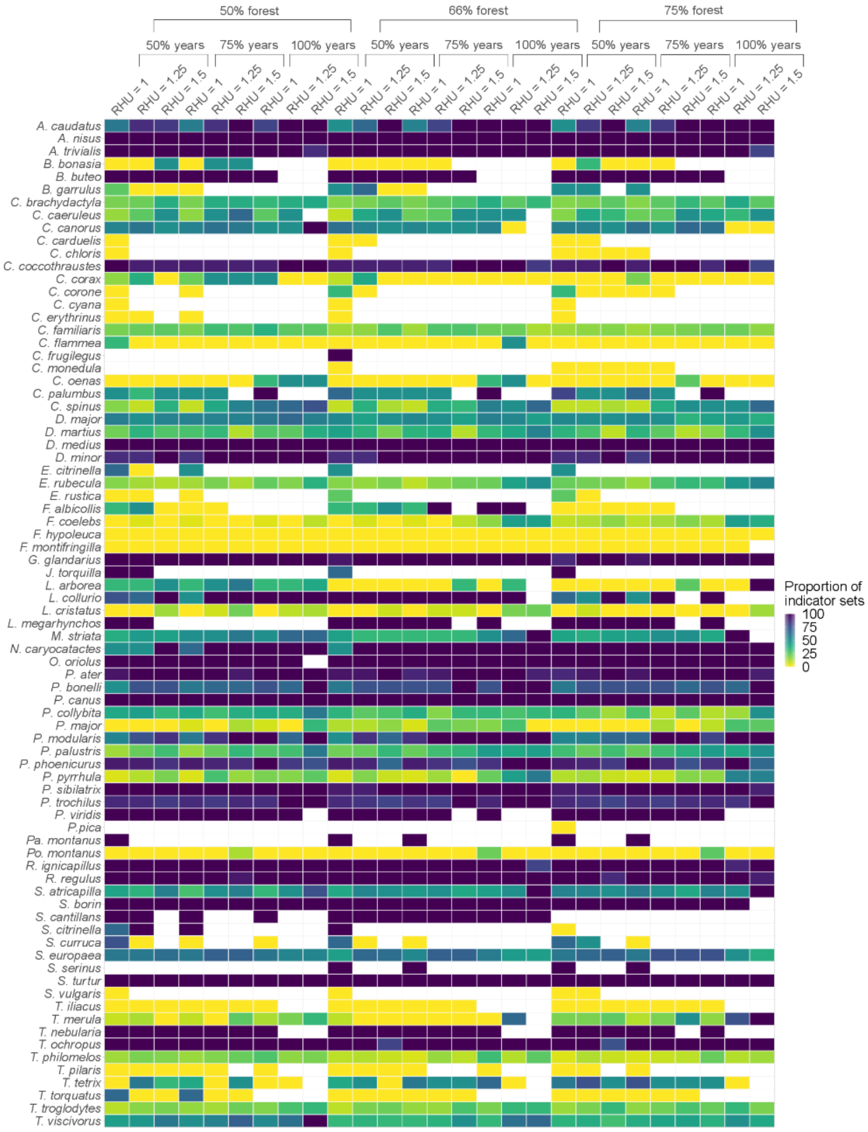


Fig. A.3.2. Proportion of indicator sets each species occurs in based on criteria set for the candidate species pool. An indicator set is selected from a candidate pool of species which meets the pre-determined criteria at a given spatial scale ("direct" indicator). From left to right, criteria increase towards more restrictive requirements. For example, on the far left, for a species to be included in a candidate species pool it must have a mean RHU ≥1 in 50% of years for sites with 50% forest cover. Conversely, on the far right, for a species to be included in a candidate species pool it must have a mean RHU ≥1.5 in 100% of years for sites with 75% forest cover.

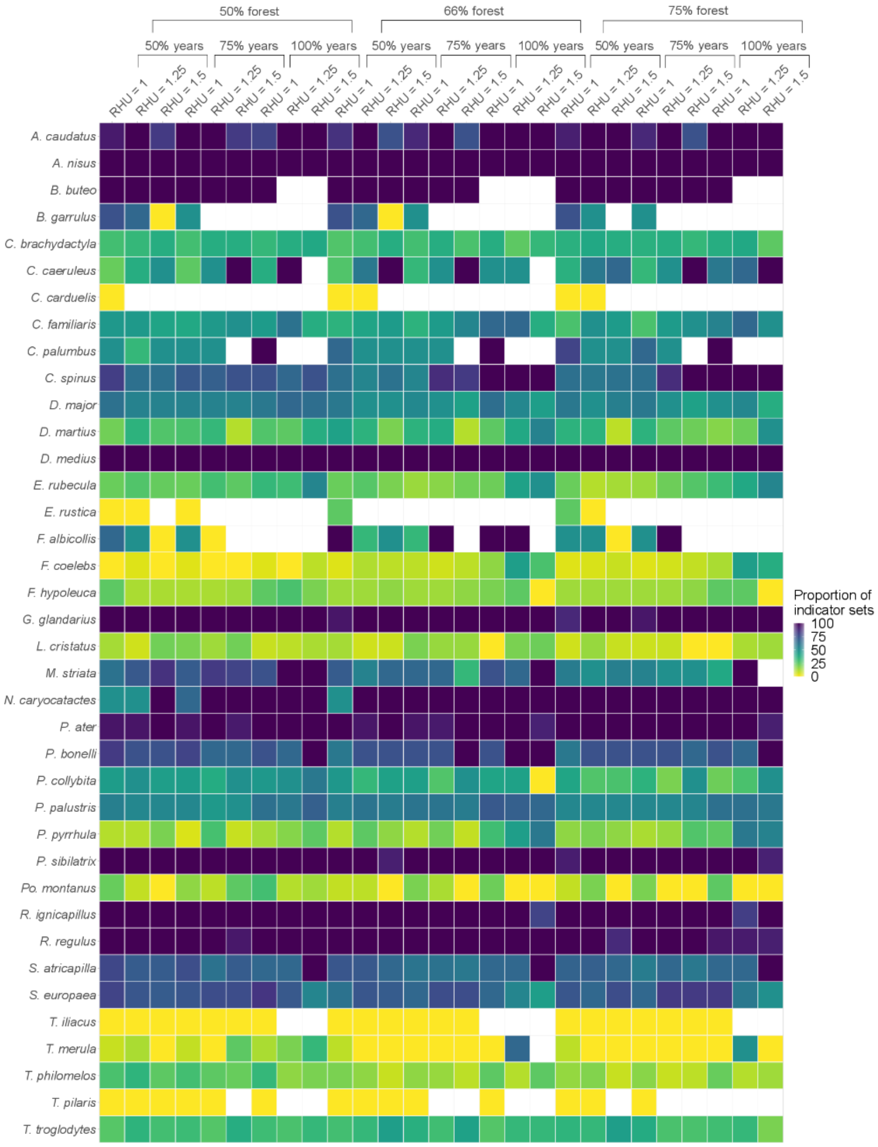


Fig. A.3.3. Proportion of indicator sets each species occurs in based on criteria set for the candidate species pool. An indicator set is selected from a candidate pool of species which meets the pre-determined criteria at a given spatial scale ("direct" indicator). From left to right, criteria increase towards more restrictive requirements. For example, on the far left, for a species to be included in a candidate species pool it must have a mean RHU ≥1 in 50% of years for sites with 50% forest cover. Conversely, on the far right, for a species to be included in a candidate species pool it must have a mean RHU ≥1.5 in 100% of years for sites with 75% forest cover. Here, early-stage forest and forest edge specialists are removed prior to producing candidate species pool.

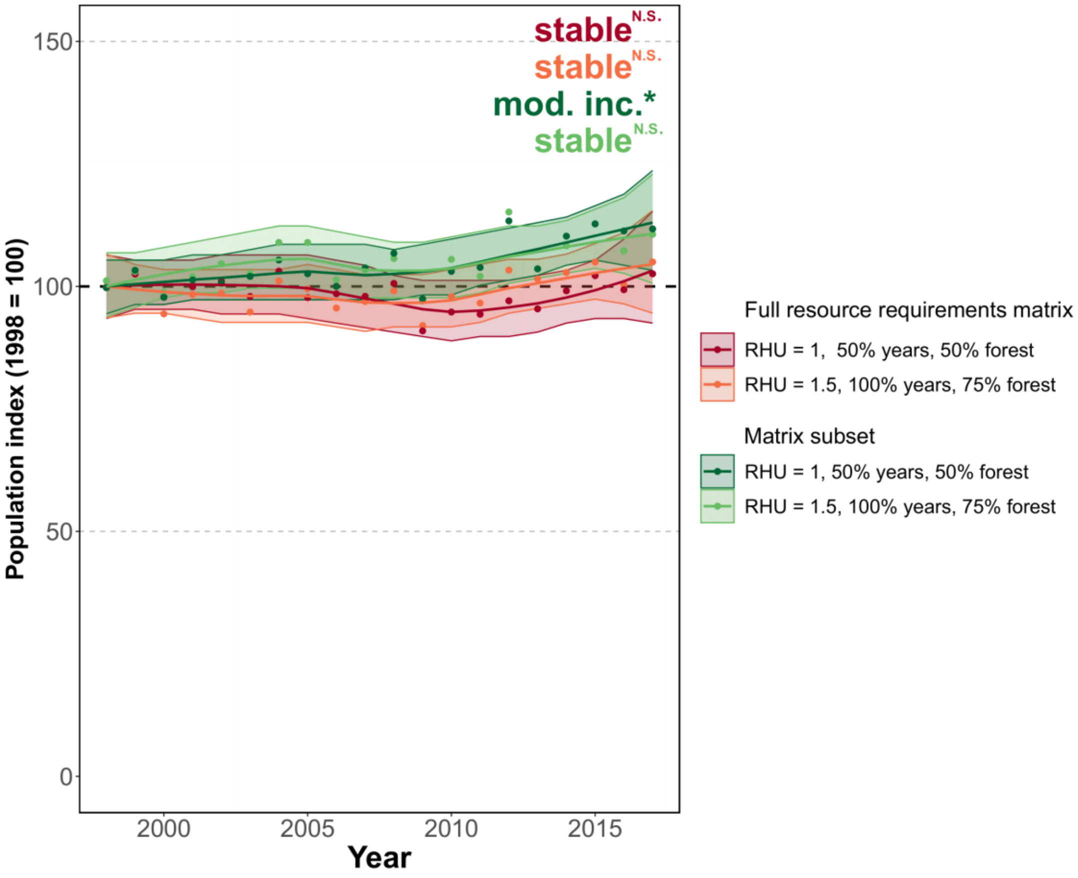


Fig. A.3.4. Smoothed pan-European multi-species indices (MSIs), with shaded 95% confidence intervals for indicator sets of forest birds. Indicator sets are selected from candidate pools of species which meet pre-determined criteria at the European level. MSIs for indicator sets which meet the most inclusive (RHU ≥ 1 in 50% of years for sites dominated by 50% forest) and most restrictive (RHU ≥ 1.5 in 100% of years for sites dominated by 75% forest) criteria are shown here as an example. Colours represent indicator sets generated from candidate species pools derived from a suite of 105 European breeding bird species (Full resource requirements matrix) or a subset of these species where early-stage forest and forest edge specialists are removed prior to candidate pool formation (Matrix subset). Description of the overall trend for each indicator are provided in the upper right corner with significance of the trend; p<0.05, *, not significant, N.S.

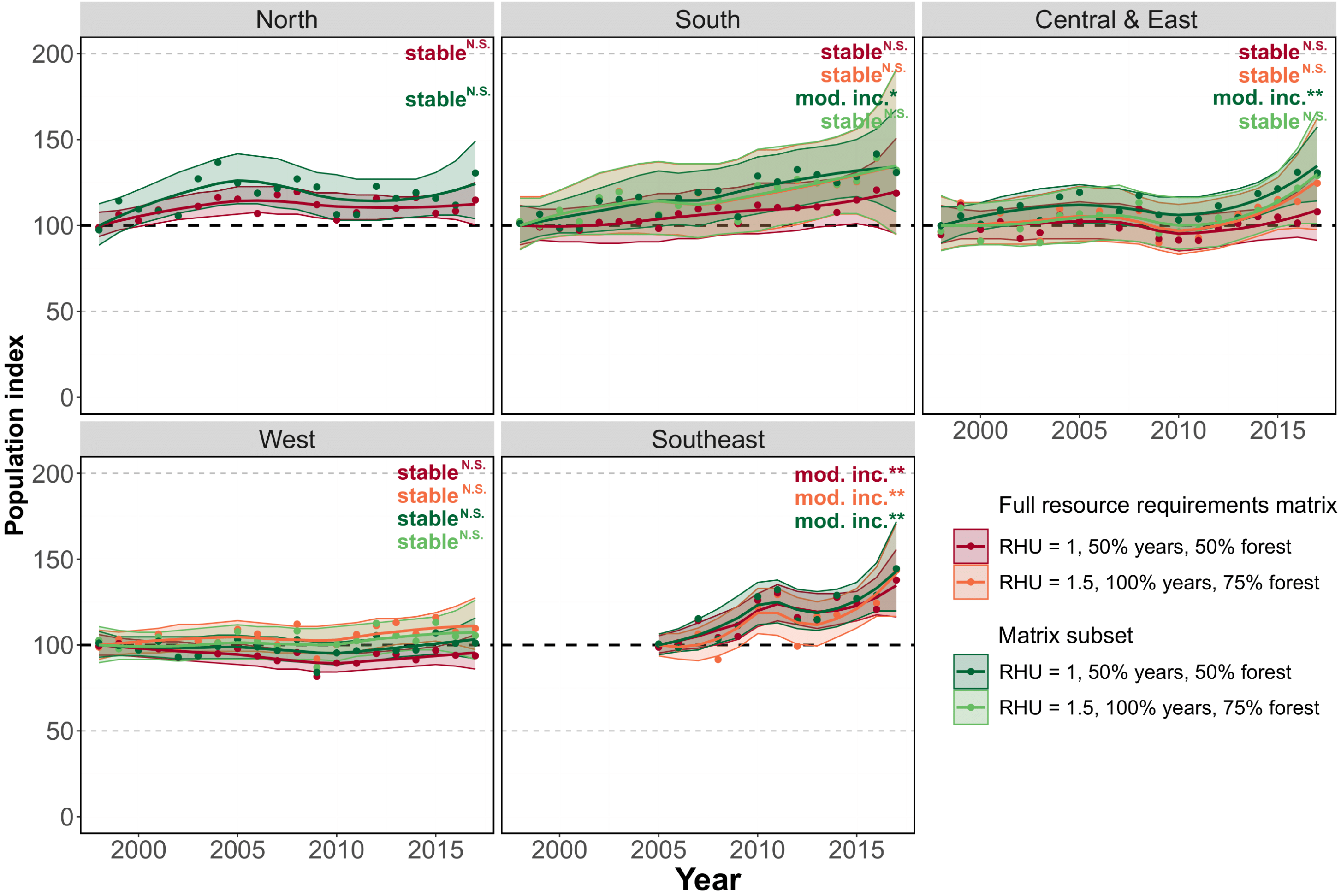


Fig. A.3.5. Smoothed regional multi-species indices (MSIs), with shaded 95% confidence intervals for indicator sets of forest birds. Indicator sets are selected from candidate pools of species which meet pre-determined criteria at the regional level. MSIs for indicator sets which meet the most inclusive (RHU ≥ 1 in 50% of years for sites dominated by 50% forest) and most restrictive (RHU ≥ 1.5 in 100% of years for sites dominated by 75% forest) criteria are shown here as an example. Colours represent indicator sets generated from candidate species pools derived from a suite of 105 European breeding bird species (Full resource requirements matrix) or a subset of these species where early-stage forest and forest edge specialists are removed prior to candidate pool formation (Matrix subset). Fewer trends are shown for North and Southeast as indicator sets with the criteria were not available. Description of the overall trend for each indicator are provided in the upper right corner with significance of the trend; p<0.01, **, p<0.05, *, not significant, N.S.

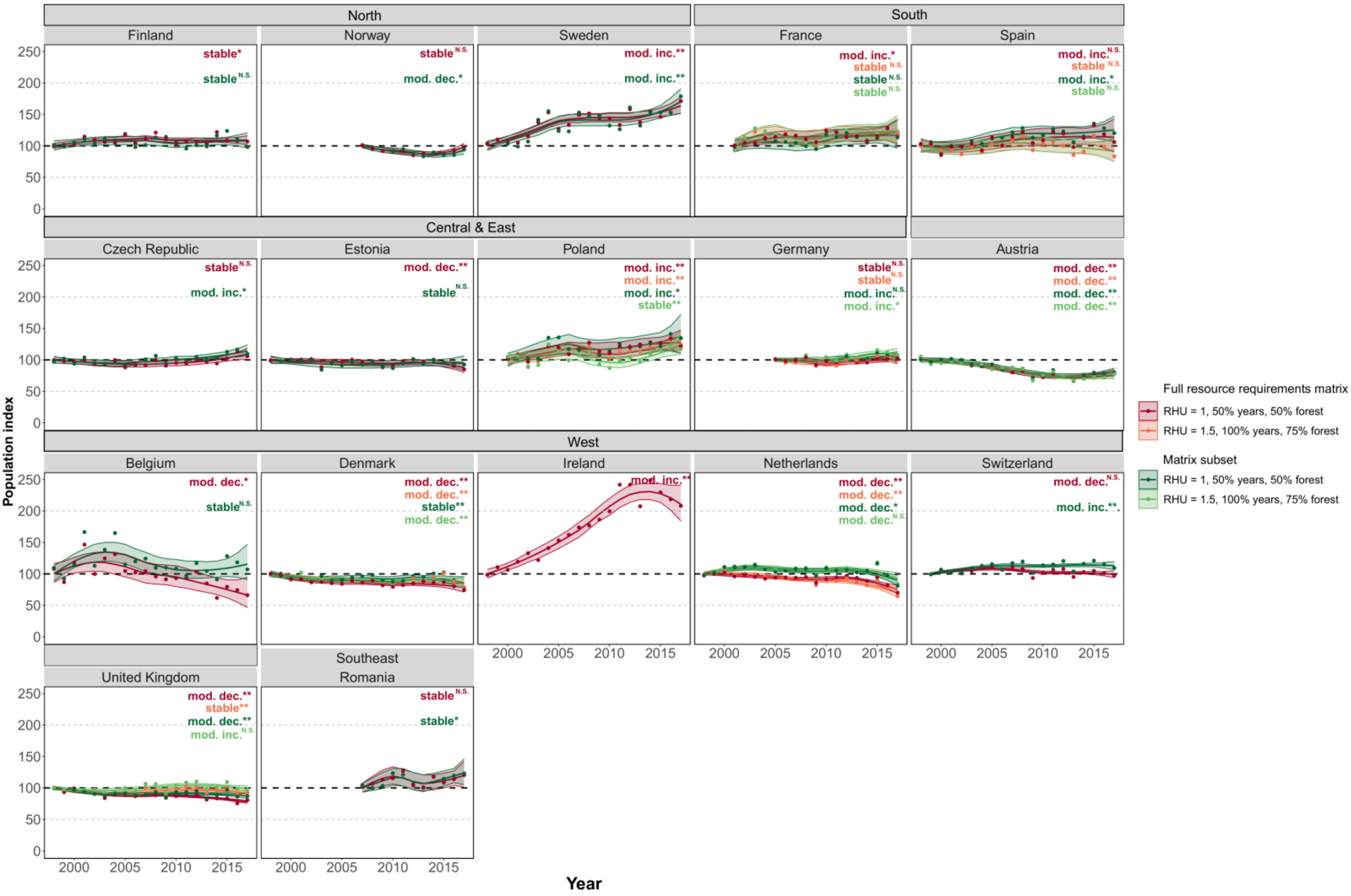


Fig. A.3.6. Smoothed national multi-species indices (MSIs), with shaded 95% confidence intervals for indicator sets of forest birds. Indicator sets are selected from candidate pools of species which meet pre-determined criteria at the national level. MSIs for indicator sets which meet the most inclusive (RHU ≥ 1 in 50% of years for sites dominated by 50% forest) and most restrictive (RHU ≥ 1.5 in 100% of years for sites dominated by 75% forest) criteria are shown here as an example. Colours represent indicator sets generated from candidate species pools derived from a suite of 105 European breeding bird species (Full resource requirements matrix) or a subset of these species where early-stage forest and forest edge specialists are removed prior to candidate pool formation (Matrix subset). Fewer trends are shown for Finland, Norway, Sweden, Czech Republic, Estonia, Belgium, Ireland, Switzerland and Romania as indicator sets with these inclusion criteria were not available. Description of the overall trend for each indicator are provided in the upper right corner with significance of the trend; $p<0.01$, **, $p<0.05$, *, not significant, N.S.

Chapter Four: Exploring temporal and spatial patterns of functional diversity in Europe's avian communities

4.1 Abstract

Exploring temporal and spatial patterns in ecological assemblages allows policymakers and land managers to monitor the impacts anthropogenic activity, environmental gradients and conservation management have on species richness, abundance and turnover. However, in recent decades research has highlighted the relationship between biodiversity and ecosystem functioning, noting that changes in biodiversity influence ecosystem processes and service provision. Therefore, there has been a strong focus on exploring functional diversity of ecological communities in order to understand these relationships further. As birds play a vital role in ecosystem service provision *e.g.,* pollination, pest and disease control, and aesthetic and cultural importance, studying avian functional diversity can provide vital insights into ecosystem health and stability. In this study, we use large spatial scale citizen science data to compare temporal and spatial patterns in functional diversity indices for European breeding bird communities in five habitat types that dominate the European landscape; forest, farmland, urban, wetland and semi-natural. We show that functional diversity indices vary over time with the extent of this variation differing between habitats and indices. In addition, the rate of change in a given functional diversity index varies across Europe, with the extent of this variation also differing between habitats and indices. Using citizen science data supports the assessment of continent level changes in functional diversity, providing deeper understanding of the impact of human activity and habitat degradation on ecosystem functioning and service provision.

4.2 Introduction

Temporal and spatial patterns in ecological assemblages are some of the most widely explored and documented aspects of ecology (Hawkins, 2001; White *et al*., 2010). In particular, studies have monitored the impact of environmental gradients (Soininen, 2010), human-induced land use change (Hendershot *et al*., 2020) and conservation management (Pellissier *et al*., 2020;

Floigl *et al*., 2022) on species richness, abundance and turnover within ecological communities across time and space. However, in recent decades there has been a focus on measuring functional components of ecological communities, as there is a positive relationship between biodiversity and ecosystem function (Petchey and Gaston, 2006; Mouchet *et al*., 2010), with temporal and spatial changes in biodiversity influencing key ecosystem processes (Cardinale *et al*., 2012; Sol *et al*., 2020), stability (Schwartz *et al*., 2000) and ecosystem service provision (Díaz *et al*., 2006).

Functional diversity (hereafter FD) describes functional differences between species in a community (Tilman, 2001) by measuring the range, abundance and distribution of species' functional traits (Mason *et al*., 2005; Petchey and Gaston, 2006), with functional traits providing key information on a species' ecological niche (Petchey and Gaston, 2002; Villéger *et al*., 2008; Pigot *et al*., 2020; Stewart *et al*., 2022). Temporal changes to a community's occupied niche space can therefore be described by exploring patterns in the community's FD over time (Mouillot *et al*., 2013; Pigot *et al*., 2020). For example, Greenop *et al*., (2021) found that invertebrate communities contributing to aquatic functioning and pollination ecosystem services saw a decline, and then eventual increase in FD over the past 45 years in the UK. The study found that at the end of the time period, the occupied niche space of communities had been altered, with communities becoming functionally more similar. This suggests that species fulfilling ecosystem services at the start of the time period were functionally more unique compared to species at the end of the timeframe.

Spatial differences in environmental conditions influence species' abundances and distributions which, in turn, impacts the composition of ecological communities and influences patterns of FD (Luck *et al*., 2013; Morelli *et al*., 2018). For example, Lakatos *et al*., (2022) found that the effect of urbanisation on avian FD varied spatially, with urban areas that had open grassland habitat having a more positive effect on FD compared to urban sites with little to no grassland. Similarly, Lourenço *et al*., (2021) found that smaller vineyards, in a more heterogeneous landscape containing neighbouring woodland, had a greater diversity of insect-eating bird species, which contribute to pest control, compared to larger vineyards, surrounded by agricultural habitats.

Studying temporal and spatial differences in avian FD is intriguing, as birds are heavily reliant on vegetation structure and climate to determine their survival (Thuiller *et al*., 2014), breeding productivity (Riehl and Smart, 2022) and dispersal capabilities (Leon *et al*., 2022) within a given habitat. Furthermore, birds play an important functional role within ecosystems and support a number of ecosystem services (Wenny *et al*., 2011). For example, birds pollinate and disperse seeds of native plant species (Wenny *et al*., 2011; Stewart *et al*., 2022), control pests in agricultural environments (Lourenço *et al*., 2021), scavenge on carcasses, thereby limiting spread of disease, and predate on vertebrates and insects, which regulates prey density (Luck *et al*., 2013; Newbold *et al*., 2013). Additionally, birds contribute to cultural and aesthetic services, as they are often depicted in art and religion, and contribute to ecotourism through bird-watching (Sekercioglu, 2002). A study by Morrison *et al*., (2021) found that acoustic diversity and intensity of natural soundscapes, provided by bird song, has declined over the past 25 years. Loss of cultural services such as diverse soundscapes may be detrimental to human health and well-being, driving humans to become disconnected from nature (Shanahan *et al*., 2015; Gaston and Soga, 2020).

The objective of this study is to explore and compare temporal patterns in FD indices for bird communities in five habitat types that dominate the European landscape; forest, farmland, urban, wetland and semi-natural. To calculate FD indices, we use site-level bird count data from the Pan-European Common Bird Monitoring Scheme (PECBMS), which are derived from citizen-science based national monitoring schemes in Europe (Brlík *et al*., 2021). In addition, we explore these temporal patterns spatially across latitudes and longitudes, and across pre-defined European regions. Finally, we investigate the relationship between the rate of change in FD, species richness and total abundance at a site level to determine if they are positively correlated. We predict that avian FD will vary across habitats as European habitats have undergone significant changes over recent decades, with the extent of these alterations varying between habitats (García-Navas and Thuiller, 2020). In addition, we expect the rate of change in FD to vary spatially as ecological communities and the functional traits expressed by those communities are shaped by evolutionary, ecological and historical mechanisms that vary in extent and significance across landscapes (Violle *et al.*, 2014). Finally, we predict that FD and species richness will be highly correlated for FD indices that consider species richness in their calculation, and that FD and total abundance will show varied results across indices and habitats as a positive rate of change in total abundance does not assume a positive rate of change in FD (Pakeman, 2011).

4.3 Methods

4.3.1 Bird and habitat data

Annual, site-level count data was acquired from PECBMS for 448 European breeding bird species across 22 citizen-science based national monitoring schemes (21,551 sites in total). Each site was surveyed using one of three possible techniques; point count, line transect or territory mapping (Brlík *et al.*, 2021), with survey technique varying with scheme. The geographic coordinates of the centroid for each site were known, with count data from 1998 to 2017 used to ensure coverage from a representative suite of countries. 35 subspecies were grouped at species level (Handbook of the Birds of the World and BirdLife International, 2020), leaving a total of 413 species.

Next, level three habitat data were extracted from Corine Land Cover (CLC) 2012 (Copernicus Land Monitoring Service, 2012) for 1km^2 areas centred on each PECBMS survey site. As open, marine habitat was not the focus of this study, sites containing lagoons, estuaries, and/or sea/ocean habitats (687 in total) were removed from further analysis. For the remaining sites, level three CLC habitats present at each site were aggregated into five broad habitat types; forest, farmland, urban, wetland and semi-natural (Table A.4.1). The area of each of these five habitats at each site were calculated and sites were classified according to the dominant habitat type, *i.e.* that covered the largest area within each site.

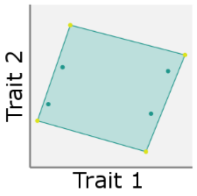
4.3.2 Measuring functional diversity

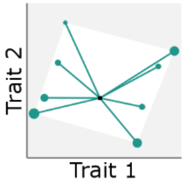
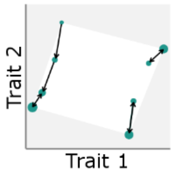
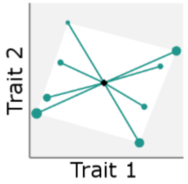
All subsequent analyses were carried out in R version 4.0.1 (R Core Team, 2020).

We compiled a range of 15 morphological and ecological avian traits which are commonly used in FD studies of bird communities (Altamirano *et al.,* 2020; Jacoboski and Hartz, 2020; Stewart *et al.,* 2022; Anderle *et al.,* 2022). These reflect diversity in species morphology, trophic niche position, diet, reproductive success, dispersal capabilities and evolutionary distinctness (Jetz *et al.*, 2014; Storchová and Hořák, 2018; Tobias *et al.,* 2022). We supplemented this trait matrix with six further traits, derived from the Relative Habitat Use (RHU) metric (Larsen *et al.*, 2011), which describe the extent of species' association with each of the five habitat types (forest, farmland, urban, wetland, semi-natural) and each species' degree of habitat specialisation (O'Reilly *et al.,* 2022) (trait definitions and further details in Table A.4.2). Due to data availability, it was not possible to calculate RHU values for any of the five habitats for 153 out of the 413 species. Although methods are in place to quantify FD when species have missing traits, (see Gower, 1971), studies suggest that FD indices can be sensitive to the completeness of a community trait matrix, especially if a high proportion of species have missing traits (Májeková *et al.*, 2016). Therefore, studies suggest removing these species from the trait matrix to ensure accurate FD indices are produced (Magneville *et al*., 2022). These 153 species were subsequently removed from the matrix and all species' data for site*year combinations in which these 153 species were recorded were also removed. The species removed were uncommon and occurred in few site*year combinations (13,026 site*year combinations and 770 sites overall) relative to the total number of site*year combinations across Europe (161,663 site*year combinations and 20,864 sites overall). Following this, sites with fewer than three years of count data were also removed. This left 260 species in the trait matrix and 15,111 sites.

Before calculating FD indices, all continuous traits were log-transformed to ensure they were normally distributed (de Bello *et al.*, 2021). All further steps to calculate FD used the mFD R package version 1.0.0 (Magneville *et al*., 2022). First, we computed a Gower species distance matrix for the trait-based distance between each pair of species, considering both continuous and categorical traits (Gower, 1971). Principal Coordinates Analysis (PCoA) was then performed to ordinate species along the major axes and plot them within multidimensional functional trait space, with each trait weighted equally. The quality.fspaces function within the mFD package was then used to evaluate the quality of the multidimensional space built by the PCoAs according to the deviation between trait-based distances and distances in functional space. From this, seven PCoA axes were identified as the optimum number to use which would ensure that trait-based distances between species were accurately represented, whilst allowing computation of FD indices (Magneville *et al*., 2022). Convex-hull based indices require a functional trait space with fewer axes than the number of species, therefore site-level data for years that had fewer than eight species were removed from further analyses. If any sites consequently fell below the inclusion threshold of three years of count data, then they were fully excluded. This left 14,454 sites for which we calculated annual FD indices; richness (FRic), evenness (FEve), dispersion (FDis), originality (FOri) and specialisation (FSpe). The functional structure of an ecological community is composed of multiple, independent aspects (Mason *et al*., 2005; Mouchet *et al*., 2010) which a single FD index cannot compute (Mouillot *et al*., 2013). Therefore, the above indices were chosen as each quantifies a slightly different aspect of FD so that, when considered together, we gain an understanding for overall FD (Table 4.1).

Table 4.1. Functional diversity indices used in this study. To further explain how each index is calculated, an exemplary simulated community is plotted in two-dimensional functional trait space according to two traits. In the context of this study, community can be described as the group of species at a given site, in a given year. Species’ distances from one another were extracted from a Principal Coordinates Analysis (PCoA). In the context of the functional richness index, yellow circles represent species on the boundaries of functional trait space. For functional evenness, dispersion, originality and specialisation, circle sizes are proportional to species’ relative abundances, and for functional originality, arrows show the direction of each species to its nearest neighbour. The final column illustrates how each functional diversity index for the simulated community could increase or decrease.

Functional diversity index	Definition	Simulated example	Index response
Functional richness (FRic) (Villéger *et al.*, 2008)	Describes the amount of functional trait space occupied by species in a community.		• Increases if a functionally unique species appears in the community. • Decreases if one of the existing species on the boundary of trait space disappears from the community.
Functional evenness (FEve) (Villéger *et al.*, 2008)	Describes the regularity with which species’ abundances are distributed in functional trait space (along the shortest minimum spanning tree linking all species).		• Increases as species’ abundances become more similar. • Decreases as the abundance of one species becomes more dissimilar to all other species in the community.

Functional dispersion (FDis) (Laliberté and Legendre, 2010)	Describes the mean distance of individual species to the centroid of all species in multidimensional trait space, weighted by species' relative abundances.		• Increases if species' abundances in the upper left or right corners increase, as the centroid will be more central to all species. • Decreases if species' abundances in the lower left or right corners increase, as the centroid is pulled towards the more abundant species.
Functional originality (FOri) (Mouillot *et al.*, 2013)	Describes the weighted mean distance of each species to its nearest neighbour in functional trait space. Distances are weighted based on species' relative abundances. Describes the isolation of a species in the functional trait space of a community.		• Increases if a functionally unique species appears in the community. • Decreases if a functionally similar species appears in the community, or if the relative abundance of one of the existing species compared to its nearest neighbour increases.
Functional specialisation (FSpe) (Mouillot *et al.*, 2013)	Describes the mean distance of a species from the rest of the species pool in functional space.		• Increases as relative abundance of functionally unique species (far from centroid) compared to that of functionally similar (close to centroid) species increases. • Decreases as the relative abundance of functionally similar (close to centroid) species compared to that of functionally unique (far from centroid) species increases.

4.3.3 Statistical analysis

4.3.3.1 European temporal trends

To account for potential differences in detectability, observer effects and differences in sampling protocols across survey schemes, we standardised FD indices at the site-level by subtracting the mean site-level index from the annual index value and dividing by the site-level standard deviation (Morrison *et al.*, 2021).

First, we considered European temporal trends for each habitat and FD index separately to look specifically at their patterns. For this, separate general linear mixed models (GLMMs) were built for each habitat and FD index in turn using the lme4 R package (Bates *et al.,* 2015) with standardised annual site-level values for the given FD index as the response variable and longitude, latitude and year (continuous) as fixed effects. Variables longitude and latitude were included to account for any geographic differences in FD. Site, year and country were included as random effects as avian communities across sites and years were not independent of one another. A likelihood ratio test was carried out on each model to test the importance of each fixed effect by comparing models with all fixed effects included to those without each term in turn. A similar study by Morrison *et al.,* (2021) using PECBMS count data tested for spatial autocorrelation of modelled residuals, separately for each year, using Moran's I. The study found significant spatial autocorrelation, however the sizes of the estimates were minor and therefore were ignored. As the data used in this study and in Morrison *et al.,* (2021) were virtually the same, we do not consider spatial autocorrelation issues further in this study.

Next, we explored differences in European temporal trends between habitats for each FD index. For this, separate GLMMs were built for each FD index with standardised annual site-level values for the given FD index as the response variable and habitat, longitude, latitude, year (continuous) and the interaction between habitat and year as fixed effects. Variables longitude and latitude were included to account for any geographic differences in FD. Site, year and country were included as random effects. A likelihood ratio test was carried out on each of these models to test for the importance of each fixed effect. Using the posthoc_Trends_Pairwise test from the grafify R package (Shenoy, 2021), we then explored differences in temporal trends between each pair of habitats to determine which were significantly different from one another.

4.3.3.2 Spatial variation in functional diversity

4.3.3.2.1 Variation across latitude and longitude

To explore how temporal patterns in each FD index within each habitat varied spatially, we used the model structure in section 4.3.3.1. with the addition of the interactions between year (continuous) and longitude, and year (continuous) and latitude as fixed effects. Interaction terms that were not significant were removed from the models. A likelihood ratio test was carried out on each model to test the importance of each fixed effect.

4.3.3.2.2 Variation across European regions

Next, for each FD index within each habitat, we compared temporal trends across regions to explore potential regional differences in FD indices. For this, we first classified each site based on the country and PECBMS region it belonged to (Table A.4.3). For each FD index within each habitat, we then built a GLMM with standardised annual site-level values for the FD index as the response variable and year (continuous), region and the interaction between these two as fixed effects. Site, year and country were included as random effects. Interaction terms that were not significant were removed from the models. A likelihood ratio test was carried out on each model to test the importance of each fixed effect. Using the posthoc_Trends_Pairwise test, we then explored differences in temporal trends between each pair of regions to determine which were significantly different from one another.

4.3.3.3 Site-level relationship between species richness, total number of individuals and functional diversity indices

Next, for each FD index within each habitat in turn, we explored the relationship between the rate of change in species richness, total number of individuals and the FD index. For this, species richness and total number of individuals recorded in each site and each year were standardised in the same manner as the FD indices in Section 2.3.1. Next, general linear models (GLMs) were built for each habitat in turn with standardised annual values for a given FD index as the response variable and year (continuous) as the fixed effect. This produced independent estimates for the rate of change in the FD index for each site. This GLM was repeated with i) standardised species richness and ii) standardised total number of individuals as the response variables instead. Next, for each FD index within each habitat in turn, a GLMM was built with the FD index rate of change at the site level as the response variable and rates of change in standardised species richness and total number of individuals and the interaction between them as the fixed effects. Country was included as a random effect. Interaction terms that were not significant were removed from the models.

4.4 Results

4.4.1 European temporal trends

Trends for four out of five FD indices in farmland habitat changed significantly over time; FRic, FDis and FSpe increased, while FOri decreased. By comparison, in forest habitat only FEve (decline) and FDis (increase) indices changed significantly. FDis and FSpe increased significantly in urban habitat, while only FOri changed significantly (decline) in both wetland and semi-natural habitats (Fig, 4.1, Table A.4.4).

In addition, trends for FD indices varied significantly between habitats (Fig. 4.1, Table A.4.5). Farmland FRic was significantly more positive than forest and semi-natural. FEve for forest was more significantly more negative than semi-natural. Urban and farmland FDis were significantly more positive than all other habitats. For the FOri index, farmland, urban, and semi-natural were significantly more negative than forest. Finally, for FSpe, urban was significantly more positive than the other four habitats. In addition, FSpe for farmland was significantly more positive than forest, wetland and semi-natural (Table A.4.6).

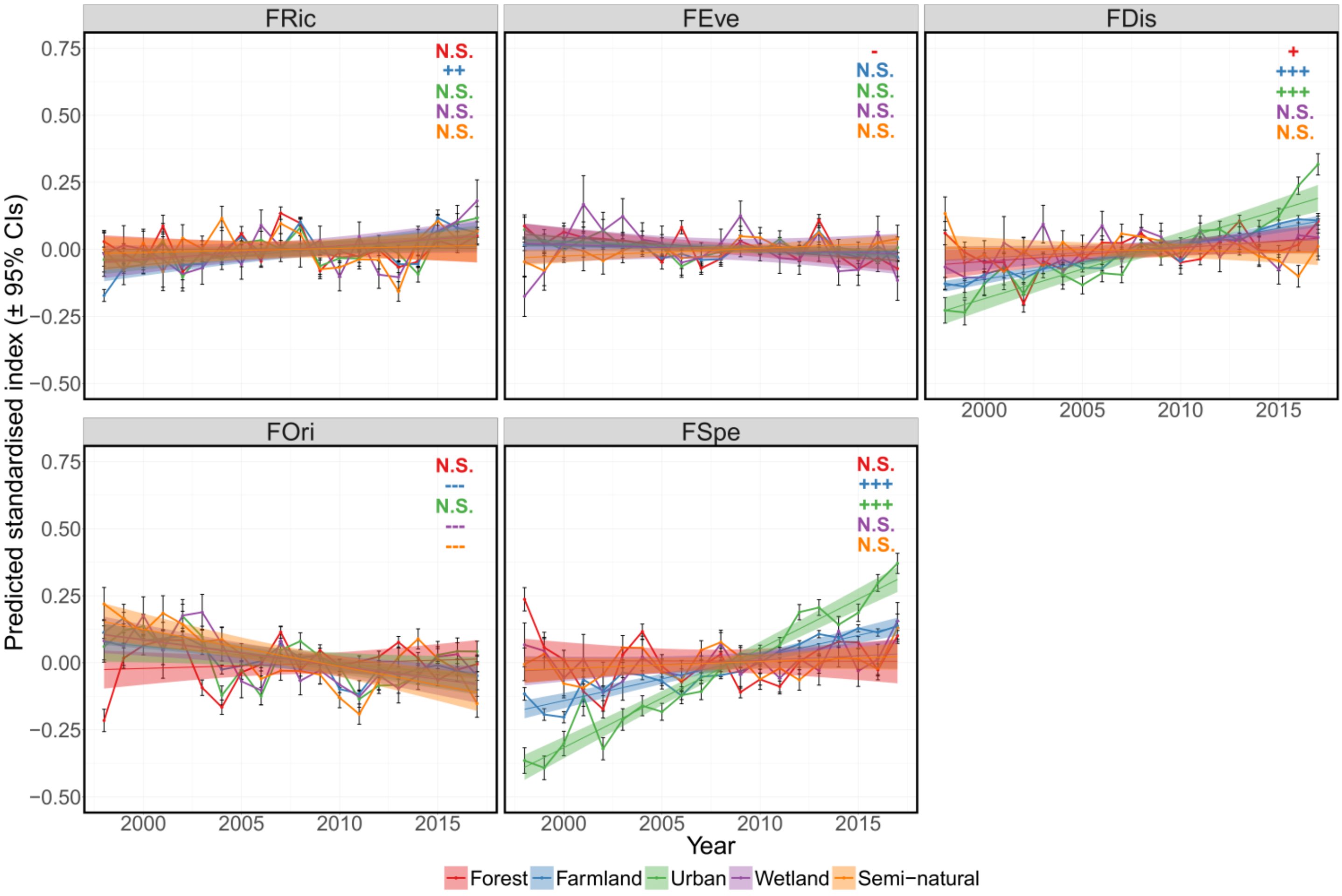


Fig. 4.1. Comparison of predicted annual variation in functional diversity indices; richness (FRic), evenness (FEve), dispersion (FDis), originality (FOri) and specialisation (FSpe) across five broad habitat types in Europe between 1998 and 2017. Annual values for each index in each habitat were standardised at the site-level prior to analyses. Lines are coloured based on the habitat with the solid straight line in each case representing the predicted trend from GLMMs (with year as continuous variable) for each index with shaded areas indicating 95%

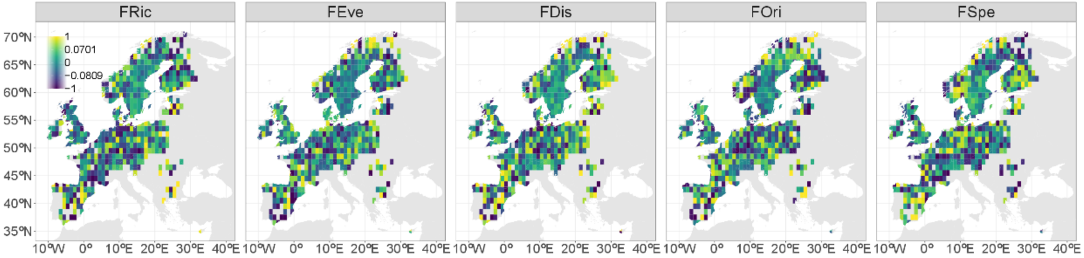
confidence intervals. Points in each panel for each habitat represent the mean annual values for the given index, with vertical lines either side of the points representing standard error for that index and habitat in that year. Significance of each trend for each habitat is provided in the upper right corner of each plot; + (positive trend with $p<0.05$), ++ (positive trend with $p<0.01$), +++ (positive trend with $p<0.001$), - (negative trend with $p<0.05$), -- (negative trend with $p<0.01$), --- (negative trend with $p<0.001$).

4.4.2 Spatial variation in functional diversity temporal trends

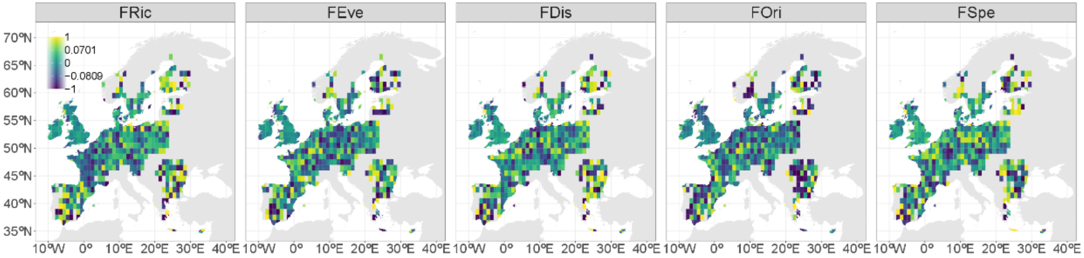
4.4.2.1 Variation across latitude and longitude

FD varied spatially across Europe with the extent of this variation differing between FD indices and habitats (Fig. 4.2, Fig. A.4.1, Table A.4.7). Across habitats, FRic tended to be higher in the East and lower in the West, except for wetland habitat which showed the opposite trend. By comparison, FEve tended to be lower in the East and South and higher in the West and North, except again for wetland which was higher in the South and lower in the North. FDis and FOri showed opposing trends to FEve and tended to be higher in the East and South, and lower in the West and North, except for urban FDis which was higher in the West and lower in the East. Finally, FSpe tended to be higher in the East and North and lower in the West and South.

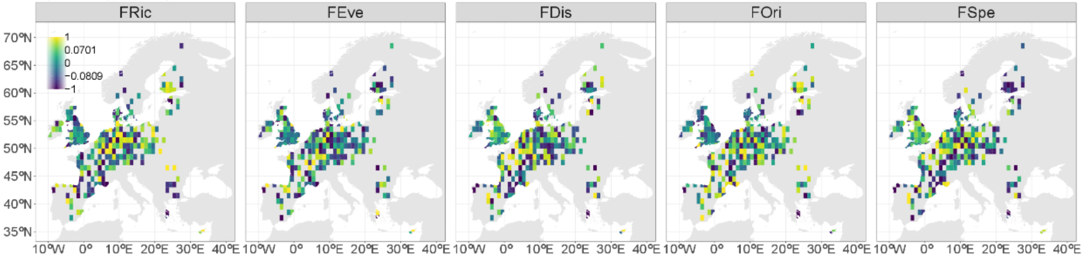
A) Forest (N=3264)



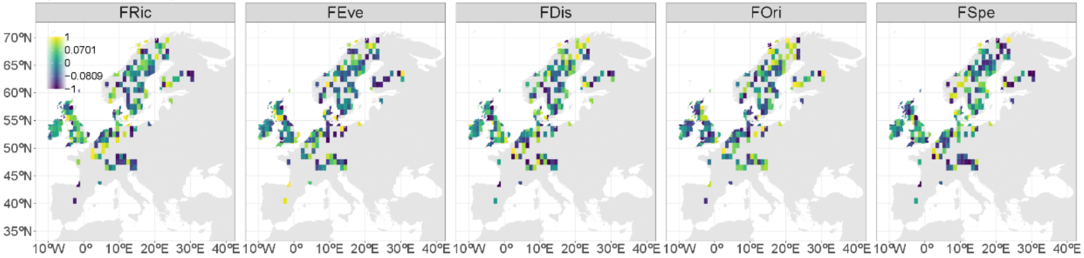
B) Farmland (N=7904)



C) Urban (N=1513)



D) Wetland (N=572)



E) Semi−natural (N=1201)

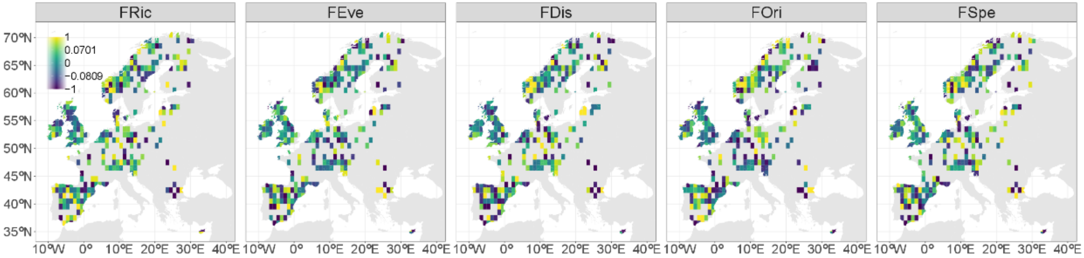


Fig. 4.2. Mean rate of change in functional diversity indices; richness (FRic), evenness (FEve), dispersion (FDis), originality (FOri) and specialisation (FSpe) in 1° x 1° grid squares across five broad habitat types in Europe between 1998 and 2017. Site-level rate of change was derived from changes in standardised annual values of each functional diversity index. Number of sites of each habitat type are shown alongside the corresponding habitat.

4.4.2.2 Variation across European regions

In all five habitats, there were significant differences in indices' trends between regions (Fig. 4.3, Table A.4.7). The extent of these differences in trends varied with habitat and FD index (Table A.4.8, A.4.9). Generally in FRic and FDis across all habitats, trends for Central & East, North and East Mediterranean were more positive than other regions. By comparison, in FEve and FSpe, trends for Central & East and North tended to be more negative than other regions. In FOri, trends for South tended to be more positive than other regions.

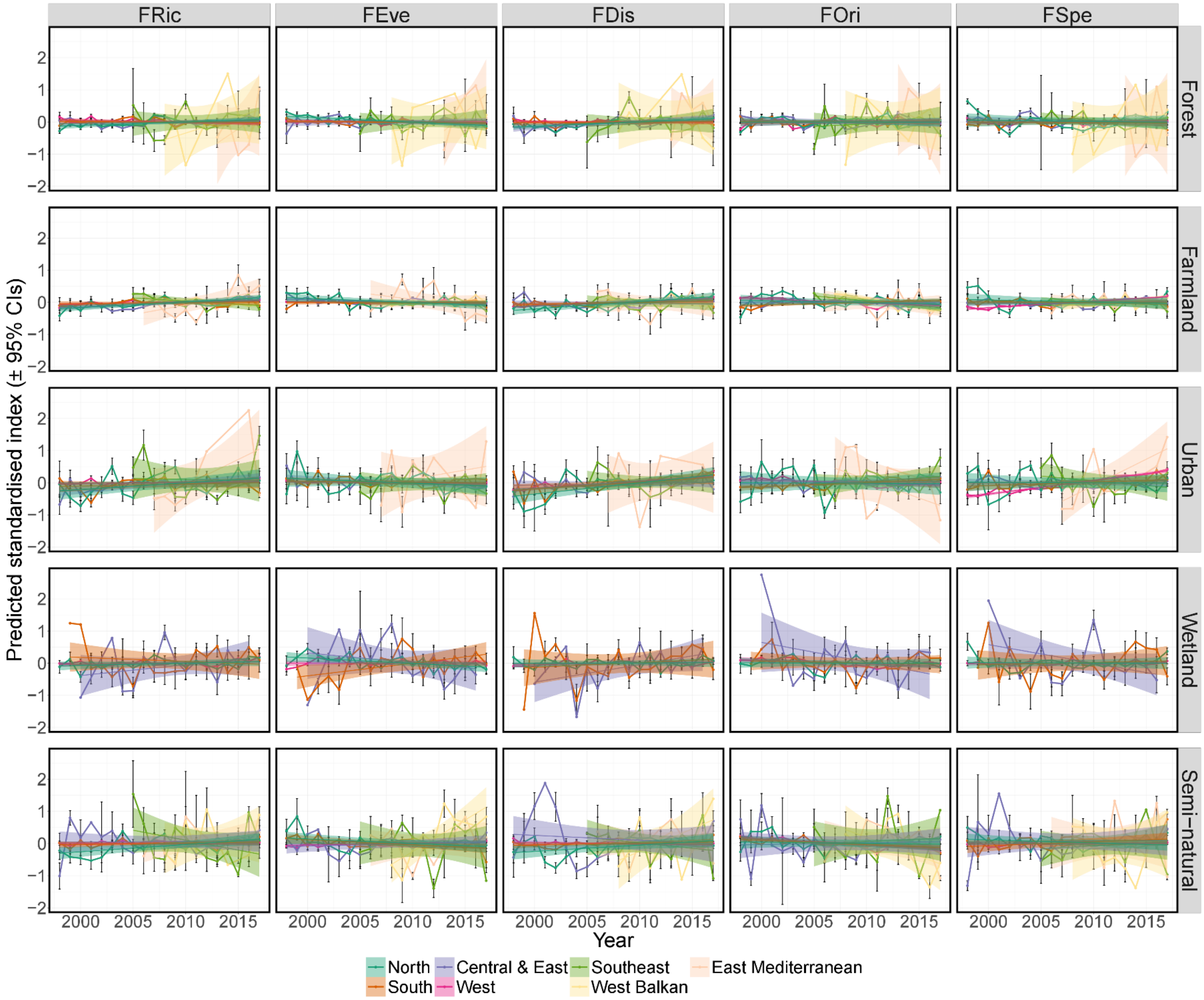


Fig. 4.3. Comparison of predicted annual variation in functional diversity indices; richness (FRic), evenness (FEve), dispersion (FDis), originality (FOri) and specialisation (FSpe) across seven PECBMS regions in five broad habitat types between 1998 and 2017. Trends for some regions are shorter as there were fewer years of site-level count data available for the countries in these regions. Annual values for each functional diversity index, in each habitat and each region were standardised at the site-level prior to analyses. Lines are coloured based on the region with the solid straight line in each case representing the predicted trend from GLMMs (with year as continuous variable) for each index, in each habitat, with shaded areas indicating 95% confidence intervals. Points in each panel for each region represent the mean annual values for the given index, with vertical lines either side of the points representing standard error.

4.4.3 Site-level relationship between total number of species, individuals and functional diversity indices

Across all five habitats, there was a significant relationship between site-level trends in FD, species richness and total number of individuals, with the extent of this relationship varying between habitats and FD indices (Fig. 4.4, Table A.4.10). Generally, a positive site-level trend in FD was associated with a positive site-level trend in species richness, except for FOri where it was more often associated with a negative FD site-level trend. The relationship between site-level trends in total abundance and FD showed greater variation between habitats and FD indices. For FRic and FOri, total abundance and FD were generally positively associated, while FEve, FDis and FSpe were more often negatively associated with total abundance.

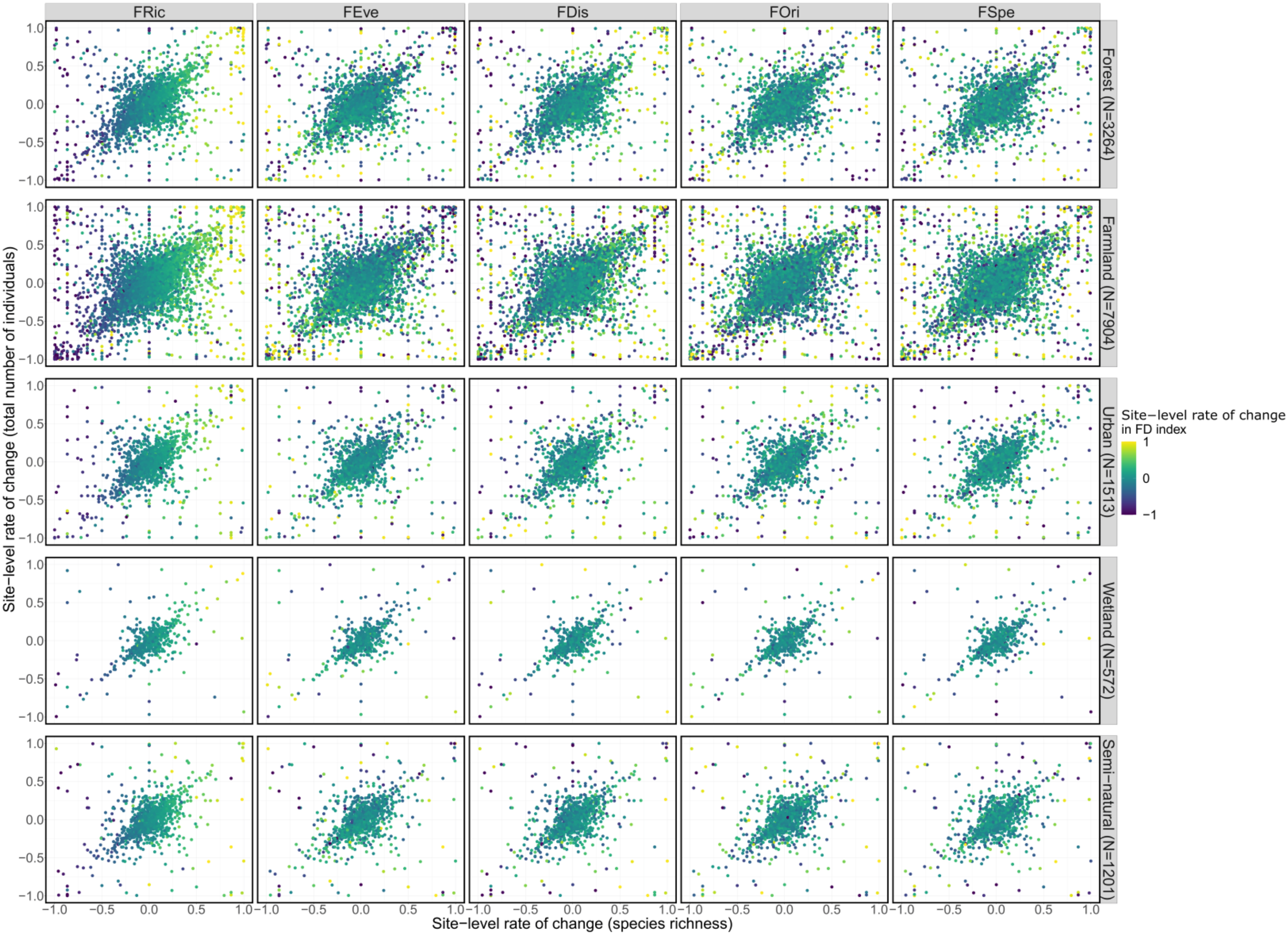


Fig. 4.4. Association between site-level trends in total number of species and total number of individuals in five broad habitat types across Europe. Colours represent site-level trends in functional diversity indices; richness (FRic), evenness (FEve), dispersion (FDis), originality (FOri) and specialisation (FSpe). Site-level trends were derived from changes in standardised annual values of total number of species, total number of individuals and each functional diversity index. Number of sites of each habitat type are shown alongside the corresponding habitat.

4.5 Discussion

Our study finds that functional diversity of European breeding bird communities has changed over the past 20 years in Europe, with the extent of this change varying between habitats and geographic location. Furthermore, we find that generally there is a positive relationship between site-level trends in species richness and FD. However, in some scenarios, site-level trends in species richness and/or abundance are negatively associated with a given FD index. Overall, these results suggest that temporal and spatial patterns in FD indices' are not universal across habitats, and that changes in FD are dependent on community-specific changes in composition associated with habitat type, local-level landscapes and environmental conditions within those landscapes.

While FD indices' for forest, farmland and urban either increase or decrease, wetland and semi-natural habitats showed only declines in FD over time. Natural grasslands, and moorland and heathland make up the largest proportion of semi-natural sites in this study (34.5% and 32.6% respectively), followed by transitional woodland (14.8%). In addition, peatland and inland marshes make up the majority of wetland sites in this study (75%). Therefore, FD of bird communities within semi-natural and wetland habitats are likely driven by patterns found in sites containing natural grasslands, moors or heath, and peatland and inland marshes respectively. In Europe, grassland extent and integrity have declined in recent decades due to widespread conversions to cropland (Bengtsson *et al.*, 2019), urban expansion and declines in traditional land use practices (Boch *et al.*, 2020), causing declines in species diversity and abundance (Fig. A.4.2) (Bengtsson *et al.*, 2019; Boch *et al.*, 2020). Similarly, declines in heathland habitat quality due to land use change, vegetation composition alterations due to rural abandonment and presence of invasive species have been linked to biodiversity loss (Fagúndez, 2013). In addition, agricultural intensification in upland moors (Reed *et al.*, 2009) has had a negative effect on breeding bird populations due to soil erosion and declines in moorland habitat quality, in particular blanket peats (Sim *et al*., 2005; Holden *et al*., 2007). Similarly, in wetland habitats, peatland and inland marshes have experienced extensive drainage for use in agriculture, forestry or peat extraction (Fraixedas *et al*., 2017; Craft, 2022), which has a negative effect on biodiversity (Hansson *et al*., 2005) and avian specialists in particular (Pearce-Higgins and Grant, 2006; Fraixedas *et al*., 2017). Declines in FOri, species richness and total abundance (Table A.4.11, Fig. A.4.2) in both semi-natural and wetland habitats therefore suggest that bird communities are becoming increasingly more functionally similar over time and more functionally redundant, potentially due to these ongoing negative impacts from anthropogenic activities.

Although forested area in Europe has increased in recent decades (Schelhaas *et al*., 2003; Palmero-Iniesta *et al*., 2021), significant modifications to its composition have also occurred (McElhinny *et al*., 2005), with declines in the number of late-stage forests (O'Brien *et al*., 2021) and increases in the number of managed, early-stage plantations (Forest Europe, 2020). FD results show that abundances are unevenly distributed across species in functional trait space and that species far from the centroid of functional trait space (functionally unique) have higher abundances than species closer to the centroid (functionally similar). These patterns may be driven by an increase in the diversity and abundance of open habitat, edge and early successional species which occur due to management practices that create forest clearings, open canopy structures and complex forest mosaics (Hofmeister *et al*., 2017). The observed stability in species richness suggests species turnover in forest habitats (Söderström *et al*., 2001; Schall *et al*., 2018), with the potential arrival of generalist and loss of forest specialist species (Jones *et al.*, 2021).

Similarly we find that species richness remains unchanged over time in farmland and urban habitats, however unlike forest, three out of five FD indices in farmland and two out of five indices for urban increase significantly over time (Fig. A.4.2, Table A.4.11). This is more than any other habitat in this study. This suggests that these habitats are potentially experiencing species turnover towards species that are more functionally distinct, with functionally unique species having higher relative abundances. Extensive changes to agricultural practices across Europe in recent decades have led to increased homogenisation of the farmland landscape (Tscharntke *et al*., 2005), reduction of foraging and nesting resources for birds (Newton, 2004; McHugh *et al*., 2017), and the replacement of specialist species by generalist species (Clavero and Brotons, 2010). In accordance with the literature (Chamberlain *et al*., 2000; Donald *et al*., 2006; Brlík *et al*., 2021), in farmland sites that experience extensive agricultural intensification, we may find declines in farmland specialist diversity and abundance and increases in diversity and population sizes of generalists and/or species with dissimilar traits to farmland specialists, thereby increasing overall FD over time. However, a significant decline in FOri suggests increasing differences in abundance between functionally similar species over time. This may potentially be due to competition for resources between species that fill similar niche space, which is likely to occur in intensively managed and homogenised farmland landscapes. Increases in FD can also be associated with abandonment of rural agricultural land which occurs in some parts of Europe, most notably the South. Abandoned agricultural land encourages growth of natural vegetation, shrubs and trees over time (Rey Benayas, 2007; García-Navas and Thuiller, 2020), which creates additional habitats capable of supporting a diverse group of species (Šumrada *et al*., 2021). This displaces species associated with open or ecotone habitats *i.e.*, farmland specialists (Zakkak *et al*., 2015) and positively influences generalists (Šumrada *et al*., 2021).

In this study, each site is defined by the dominant habitat based on habitat classifications from CLC 2012. Therefore, a static habitat classification is assigned to each site and does not change over time. In the case of abandoned agricultural land, the transition from a primarily farmland site to one containing a larger proportion of vegetation, trees or shrubs is therefore not detected.

Similarly, ongoing urbanisation causes constantly changing, highly diverse habitats to occur within the urban landscape (Forman, 2014). Therefore, a static habitat classification will not detect habitat changes caused by urbanisation. Therefore we can assume that as urbanisation and urban expansion has continued over recent decades, the diversity of habitats created in this process such as parks, gardens, ponds, lakes and human settlements (Niemelä, 1999; Forman, 2014), which each supports a particular suite of species, has also increased over time. FD results show that within urban bird communities, functionally distinct species have higher abundances than functionally similar species over time. This may be due to greater habitat diversity within urban landscapes supporting a more diverse suite of species. However, we also find that the total number of individuals in urban habitats has declined significantly over time suggesting that functionally distinct species only have higher abundances relative to the rest of the community as the rest of the community is declining in abundance. Although urban habitats create a diversity of habitat types, they are limited in the population sizes they are capable of supporting.

Our study finds that there is significant spatial variation across Europe and between predefined PECBMS regions for site-level trends in FD indices over the past 20 years, with the extent of this spatial variation differing between habitats. This may be due to spatial and temporal variation in the extent of habitat management, types of management practices and environmental conditions. For instance, species composition of avian communities in forests can vary spatially and temporally with differences in forest cover, fragmentation and composition due to different forest management practices across Europe. These differences cause large disparities in the type and amount of resources available to forest birds across landscapes over time (Tellería *et al*., 2003; Basile *et al*., 2021), which are intensified by temporal and spatial differences in land-use and climate change (Lemoine *et al*., 2007). Similarly, farmland biodiversity can vary spatially in response to differences in agricultural management (Hawkins, 2001; Robinson and Sutherland, 2002), with management practices changing significantly over time and space (Chamberlain *et al*., 2000), and spatial differences in management practices having varied effects on different bird species (Kleijn and Sutherland 2003). In urban habitat, spatial variation in site-level trends may be due to spatial differences in the rate of urbanisation occurring across European cities and towns. Similarly in wetland habitat, local-level differences in size, composition, complexity (Junk, 2022), abiotic and biotic factors and management actions (Kačergytė *et al*., 2022) can result in site-level differences. Finally, the extent of management practices and composition of surrounding landscapes are likely to vary spatially and temporally for semi-natural sites (Dallimer *et al*., 2010), thereby potentially causing significant spatial variation in FD for semi-natural habitat.

In addition, we find that species richness and FD are generally positively correlated as an increase in species richness is likely to bring with it species that have unique functional traits (Cadotte *e al.*, 2011). However this pattern is not universal as the addition of a functionally similar species to a community will increase species richness but not FD (Petchey *et al*., 2007). Studies of FD are therefore more informative than simple measures of species richness when understanding the impact of anthropogenic activity on community structure (Petchey and Gaston, 2002). In contrast to this, we find more varied results when considering site-level trends in total abundance and FD. Abiotic and biotic conditions within sites influence the relative abundances of individual species (Naeem and Wright, 2003). A positive correlation between total abundance and FD can occur if specific local conditions increase the diversity of species in the site (species richness will also increase), increase the abundance of functionally unique species, or increase species' abundances in such a way that abundances are more evenly distributed across functional trait space. However, total abundance and FD can be negatively related if environmental conditions favour some species more than others, contributing to greater differences in abundances between species in a community. Monitoring FD indices which consider abundances are therefore vital when endeavouring to understand temporal and spatial changes in community functional composition.

4.6 Conclusions

In this study we find that FD indices for a given habitat vary temporally and spatially, with the extent of this variation differing between habitats and indices. If the patterns found in this study continue, we may find that increased habitat heterogeneity due to fragmentation, management practices or land abandonment will see turnover towards species with functionally unique traits and declines in species specialised to these impacted habitats. In addition, we may also see continued declines in FD within habitats that experience significant human modification and homogenisation, with greater numbers of generalists dominating avian communities. Despite most natural habitats experiencing significant land-use change and modification due to anthropogenic activities, we find that these activities do not affect all habitats equally *i.e.*, land-use change does not cause universal declines in FD. This suggests that despite declines in species richness and abundance, functional diversity and therefore ecosystem service provision may not be effected by land-use change. However, changes in community structure and species' abundances over space and time suggest that species fulfilling those functional roles within a community may be changing.

4.7 Appendices

Table A.4.1. Corine Land Cover 2012 Levels 1 – 3 with habitat category assigned to each Level 3 habitat

Assigned habitat category	Level 1	Level 2	Level 3
Urban	Artificial surfaces	Urban fabric	Continuous urban fabric
			Discontinuous urban fabric
		Industrial, commercial and transport units	Industrial or commercial units
			Road and rail networks and associated land
			Port areas
			Airports
		Mine, dump and construction sites	Mineral extraction sites
			Dump sites
			Construction sites
		Artificial, non-agricultural vegetated areas	Green urban areas
			Sport and leisure facilities
Farmland	Agricultural areas	Arable land	Non-irrigated arable land
			Permanently irrigated land
			Rice fields
		Permanent crops	Vineyards
			Fruit trees and berry plantations
			Olive groves
		Pastures	Pastures
		Heterogeneous agricultural areas	Annual crops associated with permanent crops
			Complex cultivation patterns
			Land principally occupied by agriculture, with significant areas of natural vegetation

			Agro-forestry areas
Forest	Forest and semi natural areas	Forests	Broad-leaved forest
			Coniferous forest
			Mixed forest
Semi-natural	Forest and semi natural areas	Scrub and/or herbaceous vegetation associations	Natural grasslands
			Moors and heathland
			Sclerophyllous vegetation
			Transitional woodland-shrub
		Open spaces with little or no vegetation	Beaches, dunes, sands
			Bare rocks
			Sparsely vegetated areas
			Burnt areas
			Glaciers and perpetual snow
Wetland	Wetlands	Inland wetlands	Inland marshes
			Peat bogs
		Maritime wetlands	Salt marshes
			Salines
			Intertidal flats
	Water bodies	Inland waters	Water courses
			Water bodies

Table A.4.2. Avian functional traits used to explore temporal and spatial trends in functional diversity indices; functional richness, evenness, dispersion, originality and specialisation.

Trait	**Description**	**Rationale**	**Source**	**Type of variable**
Bill length (mm)	From bill tip to skull.	Reflects the shape and size of food items captured and consumed (Díaz *et al*., 2013). Also used as a proxy to describe variation in bird calls and songs (Demery *et al*., 2021).	Tobias *et al*., (2022); Avonet database	Numerical, continuous
Bill width (mm)	Horizontally across widest part of the bill.			
Bill depth (mm)	Vertically down the bill taken in front of the nostrils.			
Tarsus length (mm)	From the base of the toes to tibiotarsal joint.	Reflects micro-habitat utilisation, foraging strategy, dispersal (Stewart *et al*., 2022).		
Kipp's Distance (mm)	Difference in length between wing length (carpal joint to tip of primary feather) and secondary length (carpal joint to tip of first secondary feather).	Reflect movement and dispersal abilities, locomotory behaviour, provide species with ability to withstand environmental changes (Luck *et al*., 2012).		
Wing length (mm)	From carpal joint to wing tip.			
Hand-wing Index (mm)	Kipp's Distance / wing length *100			
Tail length (mm)	From base of tail to tip of longest feathers.			

Weight (g)	A range of techniques including genus averages, morphological models and close relatives as proxies. Mean values were used.	Reflects key aspects of metabolic requirements, movement and foraging behaviour (Stewart *et al*., 2022). Also strongly related to resource use, foraging behaviour, reproductive output, longevity and dispersal abilities (Luck *et al*., 2012).		
Predominant locomotory niche while foraging	Combined trophic and foraging niche classifications from Pigot *et al.,* (2020). Species assigned to one of the following four niches; aerial, terrestrial, insessorial and aquatic.	Impact of birds on ecosystem function is primarily related to what they eat and how they obtain food (Luck *et al*., 2013). Related to species’ sensitivity to habitat change and resource requirements (Ding *et al*., 2013)		Categorical
Predominant diet	Each species assigned to trophic level from which they obtain at least 60% of their food resources. Species assigned to one of the following ten niches; frugivore, granivore, nectarivore, herbivore, herbivore aquatic, invertivore, vertivore, aquatic predator, scavenger, omnivore (uses multiple niches in equal proportions).			
Migratory status	Each species assigned to one of the following three migratory strategies; sedentary, partially migratory (undergoes short-distance migrations), migratory (long-distance migrations).	Reflects mobility, dispersal capabilities and species ability to adapt to land use change and reduce likelihood of extinction (Sekercioglu, 2012).		
Nest type	Each species assigned to one of the following five nest types; ground, ground close (nest in tussock close to ground), hole (in dead or live tree, bank or ground), open-arboreal (cup in bush, tree, cliff edge), closed-arboreal.	Reflects diversity of habitat use by species. Represents breeding ecology and niche of each species (Pearman *et al*., 2014).	Storchová and Hořák, (2018)	Categorical
Reproductive output	Annual number of clutches x clutch size x egg volume. Egg volume calculated as (0.5 x egg length x egg width)^{2}	Measure of reproductive success. Reflects reproductive strategy and species ability to recover from disturbance *i.e.*, species with larger clutches and more clutches per year will	Petchey *et al*., (2007); Storchová and Hořák, (2018)	Numerical, continuous

		recolonize more quickly (Newbold *et al.*, 2013).		
Extent of habitat association	Species’ European mean RHU score for each of the habitat types in this study were calculated. Mean RHU score used for each species at each site determined by the dominant habitat type at that site.	Influences the spatial distribution and extent of species’ resource use for a given habitat. More specialised species are less able to respond to environmental variation (Sol *et al.*, 2002).	Following the methods of O’Reilly *et al.*, (2022), scores were calculated as part of this study	Numerical, continuous
Degree of habitat specialisation	Number of habitats for which each species had a mean European RHU score of ≥1. Degree of habitat specialisation was between one and four.			Categorical
Evolutionary distinctness score	Species-level measure representing the weighted sum of the branch lengths along the path from the root of a tree to a given tip, *i.e.* species.	Reflects species’ contribution to the evolutionary history of the clade and captures uniquely divergent genomes and functions (Jetz *et al.*, 2014).	Jetz *et al.*, (2014)	Numerical, continuous

Table A.4.3. Countries in Europe with corresponding PECBMS region.

Region	**Country**
North	Finland Norway Sweden
South	France Spain
Central & East	Czech Republic Estonia East Germany Latvia Poland
West	Austria Belgium Denmark West Germany Ireland Netherlands Switzerland United Kingdom
Southeast	Bulgaria Greece Romania
West Balkan	Slovenia
East Mediterranean	Cyprus

Table A.4.4. Results of general linear mixed models (GLMMs) for temporal trends in functional diversity indices; functional richness (FRic), functional evenness (FEve), functional dispersion (FDis), functional originality (FOri) and functional specialisation (FSpe) for five broad habitat types in Europe between 1998 and 2017. Annual values for each index were standardised at the site-level prior to analyses. Significant values are highlighted in bold.

		FRic				**FEve**				**FDis**				**FOri**				**FSpe**			
Habitat	**Fixed effects**	**Estimate (SE)**	**X^2**	**df**	**p**	**Estimate (SE)**	**X^2**	**df**	**p**	**Estimate (SE)**	**X^2**	**df**	**p**	**Estimate (SE)**	**X^2**	**df**	**p**	**Estimate (SE)**	**X^2**	**df**	**p**
Forest	**Longitude**	0.00007 (0.000757)	0.0088	1	0.925	0.0001 (0.000757)	0.0168	1	0.897	-0.00008 (0.0007568)	0.0106	1	0.918	-0.0001719 (0.0007565)	0.0517	1	0.82	0.0002391 (0.0007559)	0.1000	1	0.752
	Latitude	-0.000135 (0.00104)	0.0170	1	0.896	0.00009 (0.00104)	0.0073	1	0.932	-0.0002924 (0.0010346)	0.0799	1	0.777	0.000232 (0.0010344)	0.0503	1	0.823	-0.0006099 (0.0010335)	0.3482	1	0.555
	Year	0.000194 (0.0026)	0.0056	1	0.94	-0.00497 (0.0024)	4.3019	1	**0.038**	0.0053149 (0.0026498)	4.0231	1	**0.045**	0.0019433 (0.0028959)	0.4503	1	0.502	0.0001525 (0.0033167)	0.0021	1	0.963
Farmland	**Longitude**	-0.0004823 (0.000422)	1.3062	1	0.253	0.00001 (0.000422)	0.0006	1	0.98	-0.0008597 (0.0004202)	4.1863	1	0.041	0.0007027 (0.000422)	2.7727	1	0.096	-0.0011497 (0.0004196)	7.5057	1	0.006
	Latitude	0.000447 (0.0009487)	0.2220	1	0.638	-0.00009 (0.00095)	0.0085	1	0.927	0.0004066 (0.0009468)	0.1844	1	0.668	-0.0007307 (0.0009486)	0.5934	1	0.441	0.0005475 (0.0009451)	0.3356	1	0.562
	Year	0.0067729 (0.0025652)	6.9715	1	**0.008**	-0.00109 (0.00129)	0.7139	1	0.398	0.0130848 (0.0009785)	178.8290	1	**<0.001**	-0.009618 (0.0026203)	13.4729	1	**<0.001**	0.0168703 (0.0011601)	211.4730	1	**<0.001**
Urban	**Longitude**	0.00002 (0.00113)	0.0002	1	0.989	0.0001185 (0.0011292)	0.0110	1	0.916	-0.0008578 (0.0011234)	0.5830	1	0.445	0.0006871 (0.0011343)	0.3669	1	0.545	-0.001746 (0.001103)	2.5032	1	0.114
	Latitude	0.000235 (0.00246)	0.0091	1	0.924	-0.0002189 (0.0024548)	0.0079	1	0.929	0.0017095 (0.0024356)	0.4926	1	0.483	-0.001157 (0.0024504)	0.2229	1	0.637	0.003223 (0.002399)	1.8059	1	0.179
	Year	0.00465 (0.00249)	3.4963	1	0.062	-0.002598 (0.0014845)	3.0627	1	0.08	0.022667 (0.0019624)	133.4175	1	**<0.001**	-0.0064834 (0.0036524)	3.1509	1	0.076	0.038264 (0.001451)	695.7892	1	**<0.001**

Wetland	**Longitude**	0.00008 (0.0017)	0.0021	1	0.964	-0.00007 (0.0017)	0.0018	1	0.967	0.00004 (0.0017)	0.0006	1	0.981	0.00003 (0.0017)	0.0004	1	0.984	0.00004 (0.0017)	0.0004	1	0.984
	Latitude	-0.00058 (0.00344)	0.0284	1	0.866	0.000272 (0.00344)	0.0062	1	0.937	-0.000428 (0.00344)	0.0155	1	0.901	0.00085 (0.00344)	0.0613	1	0.805	-0.000372 (0.00344)	0.0117	1	0.914
	Year	0.00443 (0.00276)	2.5762	1	0.108	-0.0014 (0.00293)	0.2294	1	0.632	0.0039 (0.00251)	2.4191	1	0.12	-0.00973 (0.00295)	10.9165	1	**0.001**	0.0034 (0.00251)	1.8300	1	0.176
Semi-natural	**Longitude**	0.00019 (0.0012354)	0.0237	1	0.878	-0.0001356 (0.0012327)	0.0121	1	0.912	0.00006 (0.00123)	0.0026	1	0.96	0.0009083 (0.0012328)	0.5428	1	0.461	-0.00001 (0.0012342)	0.0001	1	0.991
	Latitude	-0.0002804 (0.0015157)	0.0342	1	0.853	-0.0001193 (0.001508)	0.0063	1	0.937	0.00005 (0.00151)	0.0013	1	0.972	0.0002655 (0.0015132)	0.0308	1	0.861	-0.0002169 (0.0015114)	0.0206	1	0.886
	Year	0.001182 (0.0033761)	0.1226	1	0.726	0.0026863 (0.0018064)	2.2116	1	0.137	-0.00138 (0.00192)	0.5150	1	0.473	-0.013522 (0.0042237)	10.2493	1	**0.001**	0.0017878 (0.0021371)	0.6998	1	0.403

Table A.4.5. Chi^2 (X^2), degrees of freedom (df) and p-values (p) for GLMMs that compare temporal trends across five broad habitat types for each functional diversity index; functional richness (FRic), functional evenness (FEve), functional dispersion (FDis), functional originality (FOri) and functional specialisation (FSpe). Annual values for each index were standardised at the site-level prior to analyses. Significant values highlighted in bold.

	FRic			**FEve**			**FDis**			**FOri**			**FSpe**		
Fixed effects	**X^2**	**df**	**p**	**X^2**	**df**	**p**	**X^2**	**df**	**p**	**X^2**	**df**	**p**	**X^2**	**df**	**p**
Year	4.6982	1	**0.03**	2.126	1	0.145	198.8762	1	**<0.001**	11.3468	1	**0.001**	222.319	1	**<0.001**
Habitat	0.0427	4	1	0.017	4	1	0.273	4	0.991	0.1046	4	0.999	0.4782	4	0.976
Latitude	0.1337	1	0.715	0.0011	1	0.974	0.4184	1	0.518	0.6376	1	0.425	0.7463	1	0.388
Longitude	0.8197	1	0.365	0.0034	1	0.953	4.0911	1	**0.043**	2.1907	1	0.139	6.3013	1	**0.012**
Year : Habitat	26.7417	4	**<0.001**	14.8875	4	**0.005**	153.4384	4	**<0.001**	71.4715	4	**<0.001**	481.0778	4	**<0.001**

Table A.4.6. Results for pairwise comparison of temporal trends between each pair of habitats for each functional diversity index; functional richness (FRic), functional evenness (FEve), functional dispersion (FDis), functional originality (FOri) and functional specialisation (FSpe). Annual values for each index were standardised at the site-level prior to analyses. Significant values highlighted in bold.

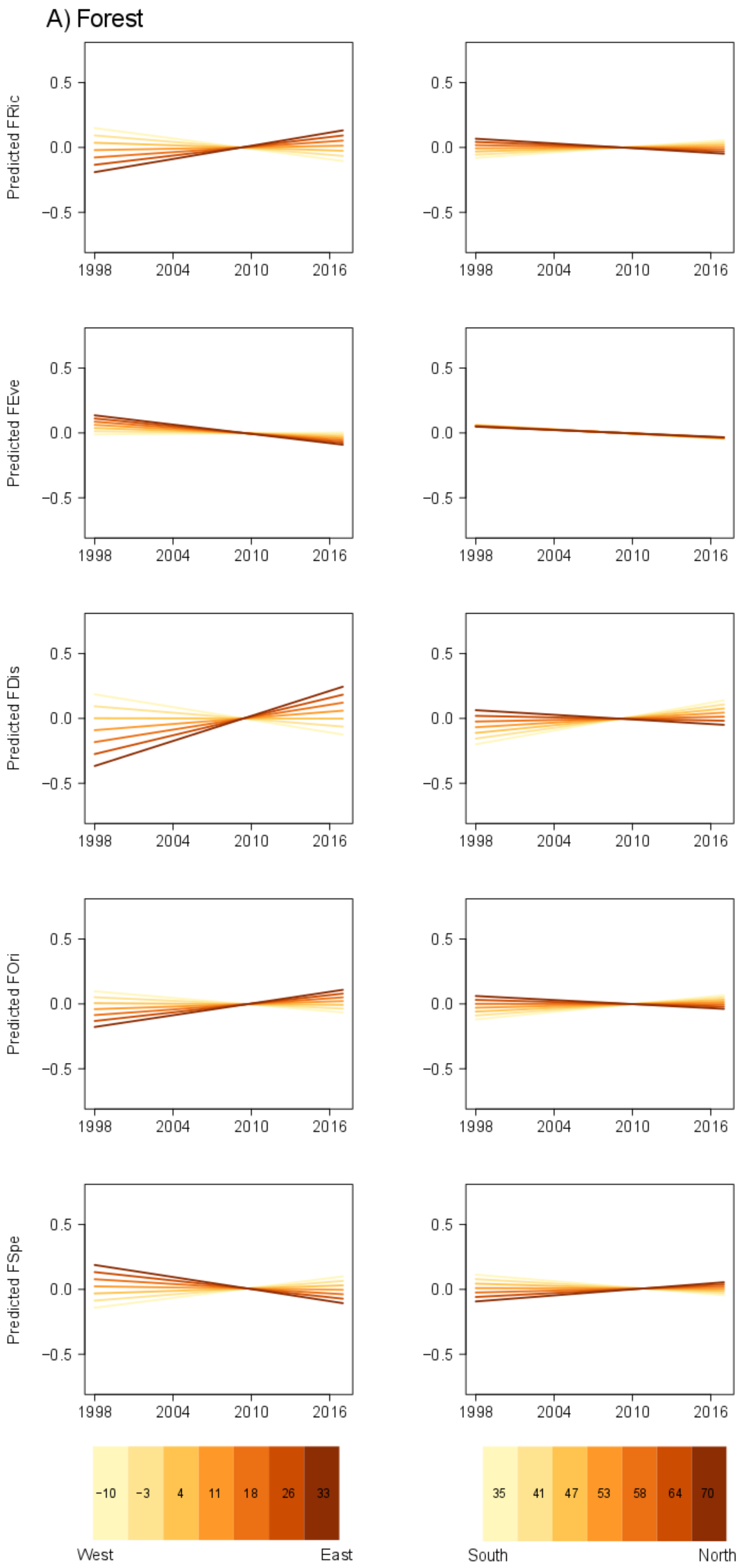
	FRic			**FEve**			**FDis**			**FOri**			**FSpe**		
Pairwise comparison	**Estimate (SE)**	**Z**	**p-value**	**Estimate (SE)**	**Z**	**p-value**	**Estimate (SE)**	**Z**	**p-value**	**Estimate (SE)**	**Z**	**p-value**	**Estimate (SE)**	**Z**	**p-value**
Wetland - Farmland	-0.0021 (0.003)	-0.798	0.996	-0.0007 (0.003)	-0.267	1	-0.0092 (0.003)	-3.562	**0.004**	-0.0003 (0.003)	-0.104	1	-0.0138 (0.003)	-5.341	**<0.001**
Wetland - Forest	0.004 (0.003)	1.468	0.784	0.0032 (0.003)	1.164	0.939	-0.0016 (0.003)	-0.601	1	-0.0105 (0.003)	-3.83	**0.001**	0.0018 (0.003)	0.646	0.999
Wetland - Semi-natural	0.0035 (0.003)	1.129	0.95	-0.0039 (0.003)	-1.267	0.899	0.0053 (0.003)	1.712	0.597	0.002 (0.003)	0.66	0.999	0.002 (0.003)	0.633	0.999

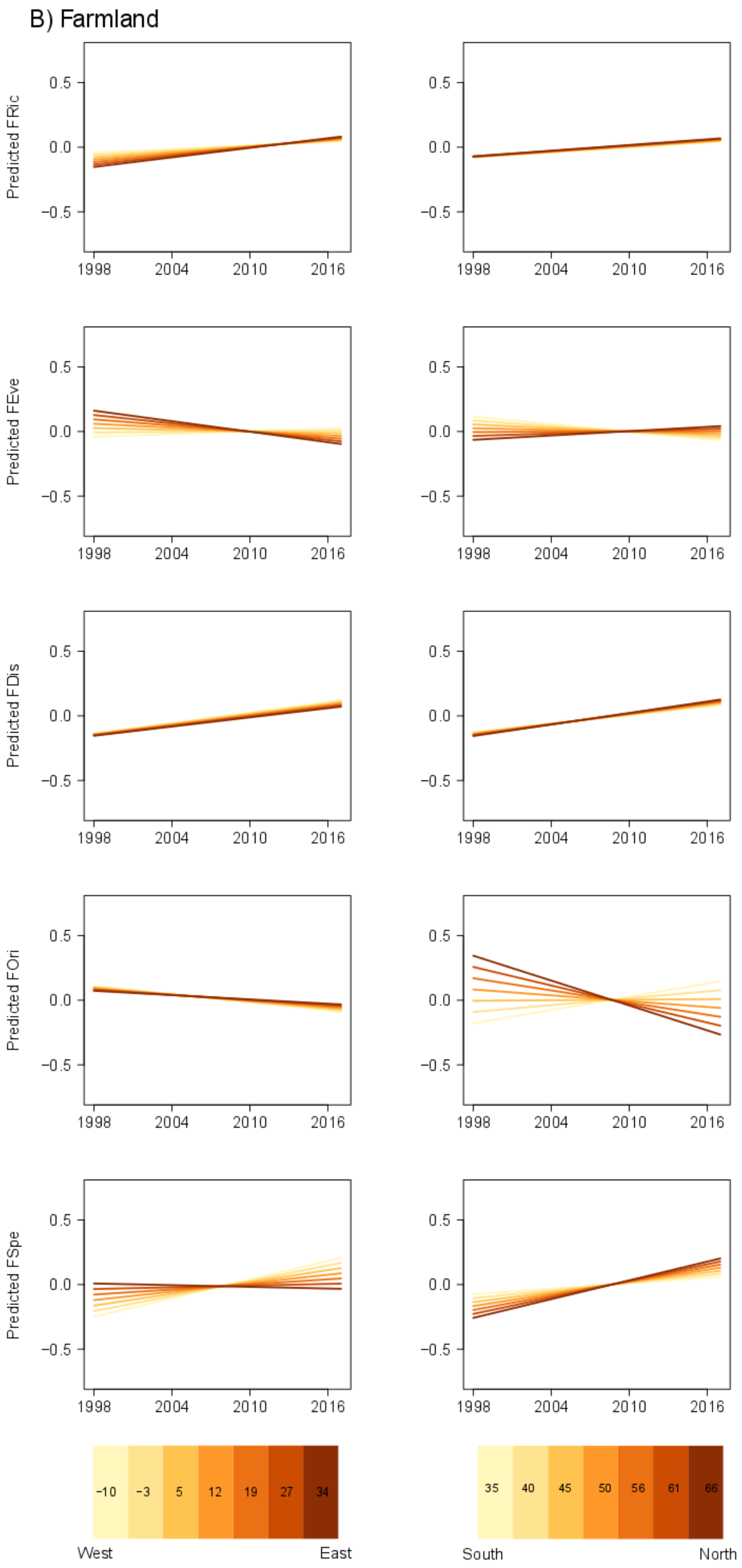
Wetland - Urban	-0.0003 (0.003)	-0.086	1	0.0013 (0.003)	0.447	1	-0.0189 (0.003)	-6.486	**<0.001**	-0.0034 (0.003)	-1.163	0.94	-0.0346 (0.003)	-11.929	**<0.001**
Farmland - Forest	0.0061 (0.001)	4.731	**<0.001**	0.0039 (0.001)	3.016	**0.025**	0.0076 (0.001)	5.904	**<0.001**	-0.0102 (0.001)	-7.943	**<0.001**	0.0156 (0.001)	12.144	**<0.001**
Farmland - Semi-natural	0.0056 (0.002)	2.89	**0.038**	-0.0032 (0.002)	-1.677	0.626	0.0145 (0.002)	7.558	**<0.001**	0.0023 (0.002)	1.2	0.927	0.0158 (0.002)	8.225	**<0.001**
Farmland - Urban	0.0018 (0.002)	1.127	0.95	0.002 (0.002)	1.235	0.913	-0.0096 (0.002)	-5.967	**<0.001**	-0.0031 (0.002)	-1.93	0.423	-0.0208 (0.002)	-12.92	**<0.001**
Forest - Semi-natural	-0.0005 (0.002)	-0.254	1	-0.0071 (0.002)	-3.358	**0.008**	0.0069 (0.002)	3.278	**0.01**	0.0125 (0.002)	5.925	**<0.001**	0.0002 (0.002)	0.088	1
Forest - Urban	-0.0043 (0.002)	-2.321	0.185	-0.0019 (0.002)	-1.026	0.974	-0.0172 (0.002)	-9.352	**<0.001**	0.0071 (0.002)	3.864	**0.001**	-0.0364 (0.002)	-19.804	**<0.001**
Semi-natural - Urban	-0.0037 (0.002)	-1.604	0.683	0.0052 (0.002)	2.239	0.225	-0.0242 (0.002)	-10.366	**<0.001**	-0.0054 (0.002)	-2.327	0.183	-0.0365 (0.002)	-15.73	**<0.001**

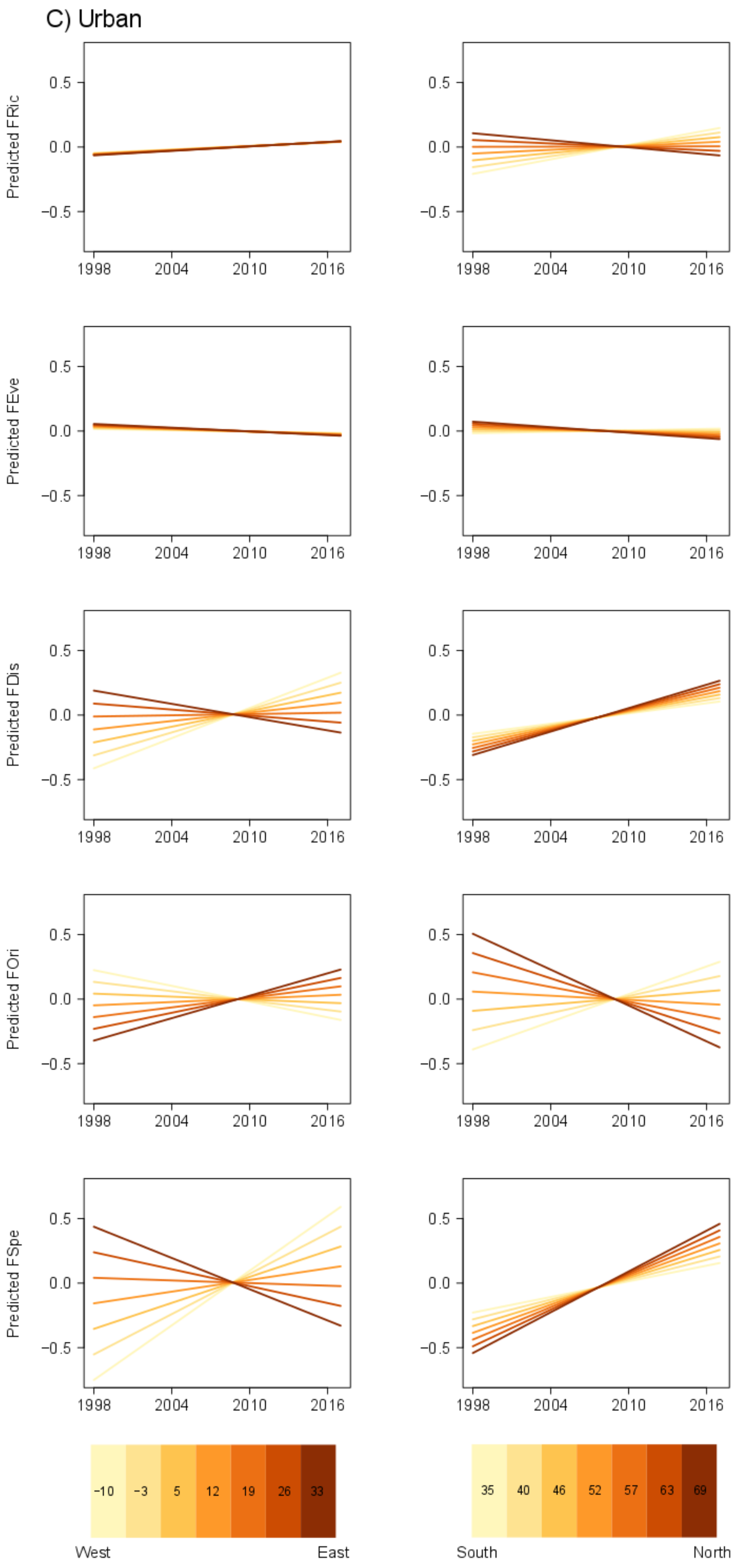
Table A.4.7. Results of GLMMs that explore spatial differences in the rate of change in each functional diversity index; functional richness (FRic), functional evenness (FEve), functional dispersion (FDis), functional originality (FOri) and functional specialisation (FSpe) for five broad habitat types in Europe between 1998 and 2017. Annual values for each index were standardised at the site-level prior to analyses. Significant values highlighted in bold.

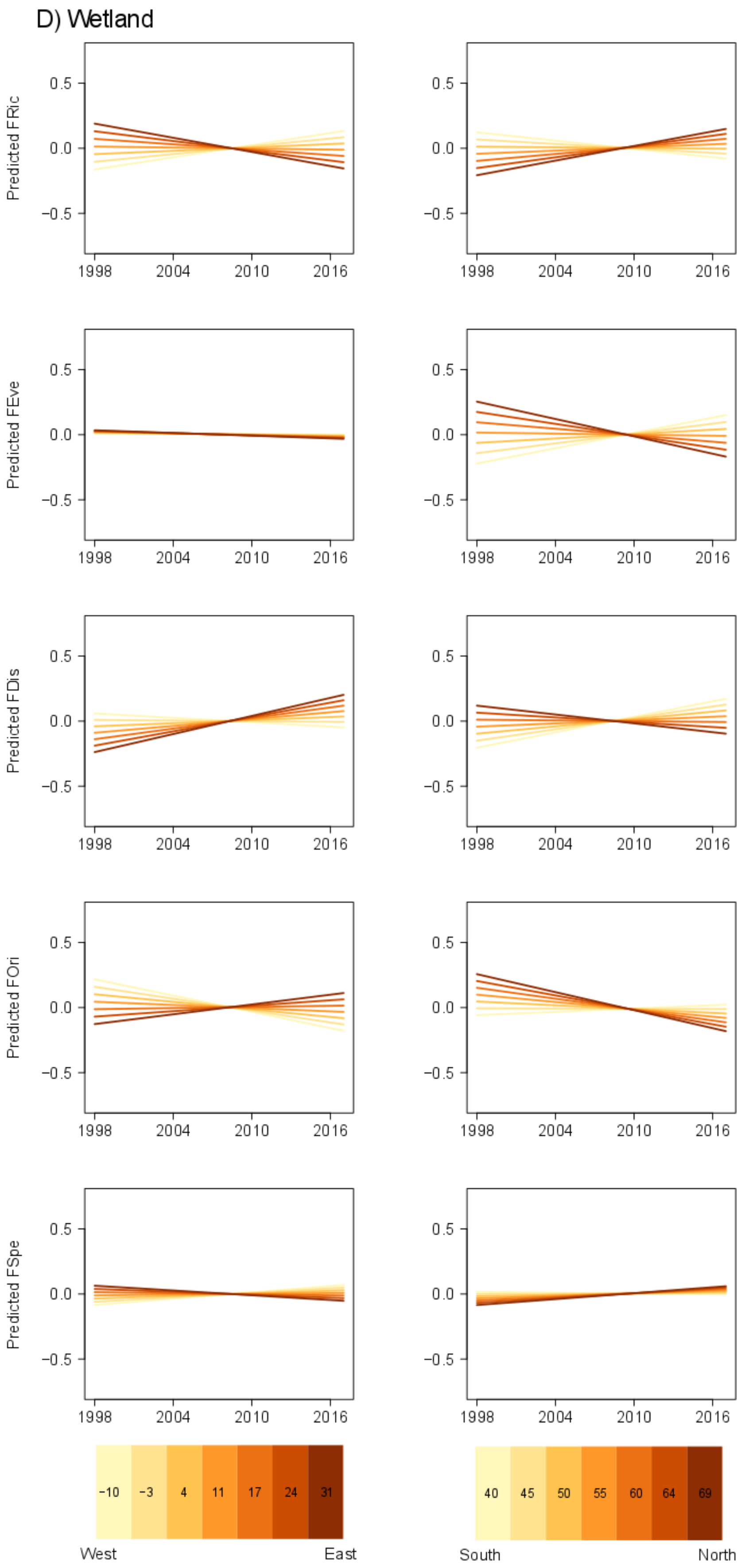
		FRic				**FEve**				**FDis**				**FOri**				**FSpe**			
Habitat	**Fixed effects**	**Estimate (SE)**	**X^2**	**df**	**p**	**Estimate (SE)**	**X^2**	**df**	**p**	**Estimate (SE)**	**X^2**	**df**	**p**	**Estimate (SE)**	**X^2**	**df**	**p**	**Estimate (SE)**	**X^2**	**df**	**p**
Forest	**Longitude**	-0.00691 (0.00171)	0.0087771	1	0.925	0.00353 (0.00171)	0.0168408	1	0.897	-0.0140158 (0.0019549)	0.007771	1	0.93	-0.0069626 (0.0019567)	0.0528657	1	0.818	0.0083439 (0.0019557)	0.0986678	1	0.753
	Latitude	-0.00006 (0.00103)	0.0037966	1	0.951	0.00005 (0.00104)	0.002712	1	0.958	0.0081186 (0.0027353)	0.030877	1	0.861	0.0055341 (0.0027374)	0.0744244	1	0.785	-0.0062978 (0.0027357)	0.4248887	1	0.515
	Year	-0.00509 (0.00284)	0.005579	1	0.94	-0.00237 (0.00266)	4.3026863	1	0.038	0.0306046 (0.0106233)	4.031697	1	0.045	0.0194844 (0.0106962)	0.450525	1	0.502	-0.0180056 (0.0108119)	0.0021169	1	0.963
	Longitude : Year	0.000568 (0.000125)	20.603986	1	**<0.001**	-0.00028 (0.000125)	4.9910963	1	**0.025**	0.0011312 (0.0001462)	59.86871	1	**<0.001**	0.0005505 (0.0001463)	14.152867	1	**<0.001**	-0.0006572 (0.0001462)	20.198051	1	**<0.001**
	Latitude : Year									-0.0006726 (0.0002052)	10.74243	1	**0.001**	-0.0004256 (0.0002054)	4.2938729	1	**0.038**	0.0004557 (0.0002052)	4.9301896	1	**0.026**
Farmland	**Longitude**	-0.00272 (0.00117)	1.3062411	1	0.253	0.0050038 (0.0011621)	0.0389158	1	0.844	-0.0008597 (0.0004202)	4.186296	1	0.041	0.0004676 (0.0004228)	1.2230898	1	0.269	0.00648 (0.00115)	6.4368776	1	0.011

	Latitude	0.000565 (0.00095)	0.3532077	1	0.552	-0.0061645 (0.0025125)	0.1240639	1	0.725	0.0004066 (0.0009468)	0.184402	1	0.668	0.0181985 (0.0025142)	0.5939188	1	0.441	-0.00638 (0.0025)	0.034455	1	0.853
	Year	0.00632 (0.00258)	6.9718409	1	0.008	-0.0251916 (0.0100847)	0.7141146	1	0.398	0.0130848 (0.0009785)	178.8290	1	<0.001	0.0715834 (0.0103267)	13.484803	1	<0.001	-0.00985 (0.01)	211.63800	1	<0.001
	Longitude : Year	0.000177 (0.00008)	4.1890686	1	**0.041**	-0.00039 (0.00009)	20.659723	1	**<0.001**									-0.000598 (0.00009)	49.278937	1	**<0.001**
	Latitude : Year					0.0004846 (0.0001933)	6.2836417	1	**0.012**					-0.001571 (0.0001933)	66.081833	1	**<0.001**	0.000545 (0.000192)	8.0280919	1	**0.005**
Urban	**Longitude**	0.00002 (0.00113)	0.000205	1	0.989	0.0001185 (0.0011292)	0.0110182	1	0.916	0.0148617 (0.0030014)	0.584265	1	0.445	-0.0138907 (0.0030954)	0.1146652	1	0.735	0.0293807 (0.0029276)	2.5256409	1	0.112
	Latitude	0.000235 (0.00246)	0.0091385	1	0.924	-0.0002189 (0.0024548)	0.0079492	1	0.929	0.0007428 (0.0024389)	0.09275	1	0.761	0.0288467 (0.0066813)	0.0262662	1	0.871	0.0013492 (0.0023936)	0.3177156	1	0.573
	Year	0.00465 (0.00249)	3.4962736	1	0.062	-0.002598 (0.0014845)	3.0626764	1	0.08	0.0263271 (0.0020646)	133.7079	1	<0.001	0.1158053 (0.0268565)	3.1595992	1	0.075	0.0455385 (0.0015773)	702.03901	1	<0.001
	Longitude : Year									-0.0012746 (0.0002257)	31.88715	1	**<0.001**	0.00115 (0.000232)	24.573307	1	**<0.001**	-0.0025251 (0.0002201)	131.56439	1	**<0.001**
	Latitude : Year													-0.0024199 (0.0005142)	22.144903	1	**<0.001**				
Wetland	**Longitude**	0.0067566 (0.0036208)	0.0021917	1	0.963	-0.0001626 (0.0017025)	0.0091229	1	0.924	0.00004046 (0.001702)	0.00056	1	0.981	-0.0067439 (0.0036176)	0.0002419	1	0.988	0.00004 (0.0017)	0.0004274	1	0.984
	Latitude	-0.0002398 (0.0034425)	0.004851	1	0.944	0.0186766 (0.0077952)	0.0053596	1	0.942	-0.0004278 (0.0034)	0.01547	1	0.901	0.0005122 (0.0034381)	0.0221904	1	0.882	-0.000372 (0.00344)	0.0117052	1	0.914
	Year	0.0065522 (0.0029561)	2.5528773	1	0.11	0.0817175 (0.0316851)	0.2376382	1	0.626	0.003903 (0.002509)	2.41913	1	0.12	-0.0118757 (0.0030856)	11.138532	1	0.001	0.0034 (0.00251)	1.8300128	1	0.176
	Longitude : Year	-0.0005918 (0.0002833)	4.3649918	1	**0.037**									0.0005999 (0.000283)	4.495011	1	**0.034**				
	Latitude : Year					-0.0015148 (0.0005752)	6.9364489	1	**0.008**												
Semi-natural	**Longitude**	-0.0061324 (0.0033491)	0.0693376	1	0.792	-0.0003323 (0.0012349)	0.0723824	1	0.788	-0.0073307 (0.0032577)	0.002437	1	0.961	-0.00626 (0.00327)	0.541839	1	0.462	-0.00001 (0.0012342)	0.0001381	1	0.991
	Latitude	0.0076743 (0.0042196)	0.0916975	1	0.762	-0.0094925 (0.0040915)	0.0062673	1	0.937	-0.0002449 (0.001514)	0.026155	1	0.872	0.000009 (0.00152)	0.00003	1	0.995	-0.0002169 (0.0015114)	0.0205988	1	0.886
	Year	0.0343612 (0.0167332)	0.1226684	1	0.726	-0.0361322 (0.0158559)	2.2129517	1	0.137	-0.0023881 (0.0019887)	0.491798	1	0.483	-0.0145 (0.00419)	10.524697	1	0.001	0.0017878 (0.0021371)	0.6998435	1	0.403
	Longitude : Year	0.0005217 (0.0002514)	4.3073082	1	**0.038**					0.0005945 (0.0002425)	6.009245	1	**0.014**	0.000575 (0.000243)	5.5865532	1	**0.018**				
	Latitude : Year	-0.0006533 (0.0003162)	4.2697228	1	**0.039**	0.0007451 (0.0003024)	6.0724296	1	**0.014**												


A) Forest
Predicted FRic
Predicted FEve
Predicted FDis
Predicted FOri
Predicted FSpe
0.5
0.0
−0.5
1998
2004
2010
2016
−10
−3
4
11
18
26
33
West
East
35
41
47
53
58
64
70
South
North


B) Farmland
Predicted FRic
Predicted FEve
Predicted FDis
Predicted FOri
Predicted FSpe
0.5
0.0
−0.5
1998
2004
2010
2016
−10
−3
5
12
19
27
34
West
East
35
40
45
50
56
61
66
South
North


C) Urban
Predicted FRic
Predicted FEve
Predicted FDis
Predicted FOri
Predicted FSpe
0.5
0.0
−0.5
1998
2004
2010
2016
−10
−3
5
12
19
26
33
West
East
35
40
46
52
57
63
69
South
North


D) Wetland
Predicted FRic
Predicted FEve
Predicted FDis
Predicted FOri
Predicted FSpe
0.5
0.0
−0.5
1998
2004
2010
2016
−10
−3
4
11
17
24
31
West
East
40
45
50
55
60
64
69
South
North

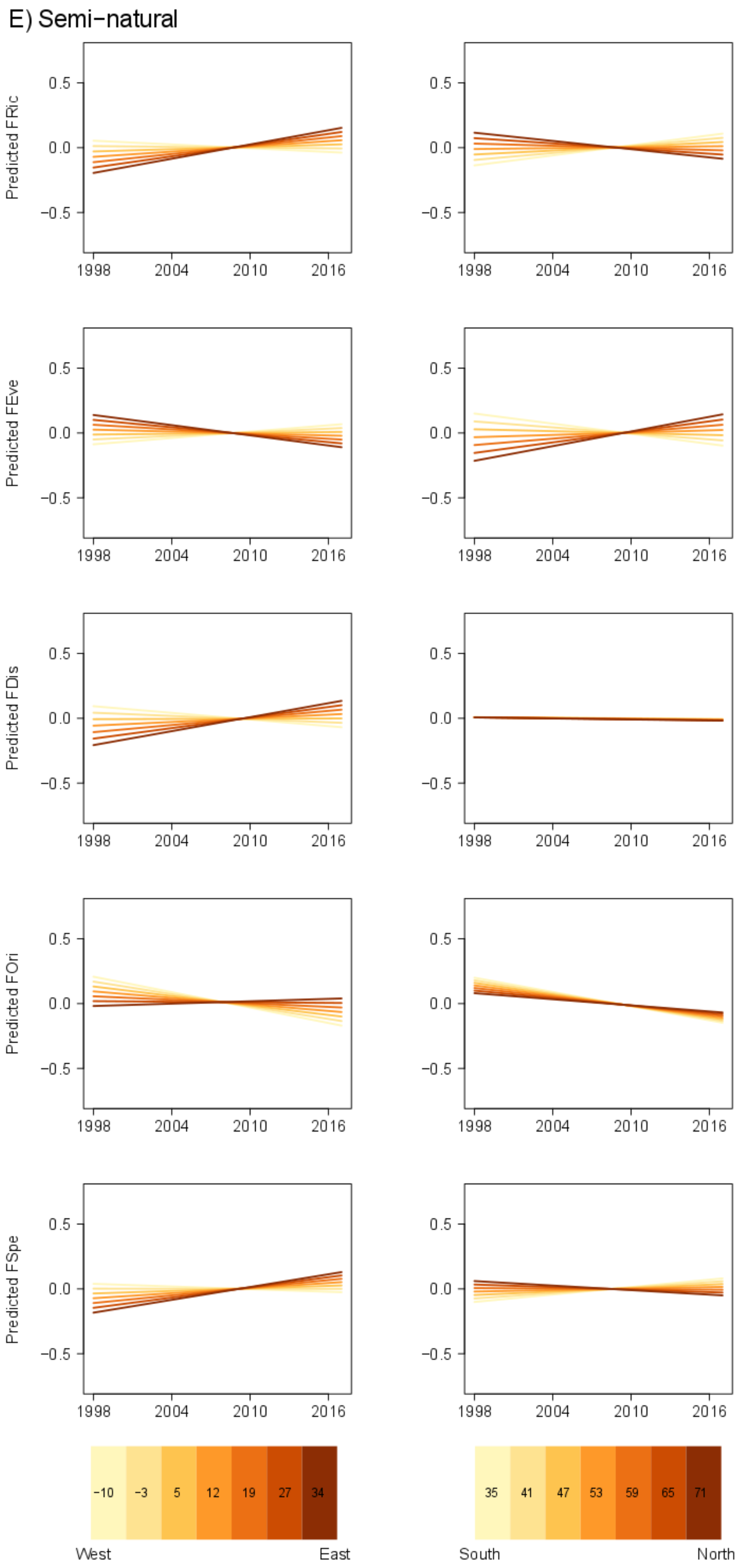

E) Semi−natural
Predicted FRic
Predicted FEve
Predicted FDis
Predicted FOri
Predicted FSpe
0.5
0.0
−0.5
1998
2004
2010
2016
−10
−3
5
12
19
27
34
West
East
35
41
47
53
59
65
71
South
North

Fig. A.4.1. Predicted rate of change in functional diversity indices for five broad habitat types in Europe between 1998 and 2017. Coloured lines indicate predicted trends at varying longitudes (left column) and latitudes (right column) at equal intervals across the range of the dataset from West and South to East and North. Predicted temporal trends reflect temporal changes in standardised functional diversity indices.

Table A.4.8. Chi^2 (X^2), degrees of freedom (df) and p-values (p) for GLMMs that explore regional differences in temporal trends in each functional diversity index; functional richness (FRic), functional evenness (FEve), functional dispersion (FDis), functional originality (FOri) and functional specialisation (FSpe) for five broad habitat types in Europe between 1998 and 2017. Annual values for each index were standardised at the site-level prior to analyses. Significant values highlighted in bold.

		FRic			**FEve**			**FDis**			**FOri**			**FSpe**		
Habitat	**Fixed effects**	**X^2**	**df**	**p**	**X^2**	**df**	**p**	**X^2**	**df**	**p**	**X^2**	**df**	**p**	**X^2**	**df**	**p**
Forest	**Year**	0.0057	1	0.94	4.475	1	0.034	4.2038	1	0.04	0.4721	1	0.492	0.0016	1	0.968
	Region	0.0197	6	1	0.4303	6	0.999	0.6323	6	0.996	0.1209	6	1	0.3789	6	0.999
	Year: Region	41.434	6	**<0.001**	17.9421	6	**0.006**	35.4991	6	**<0.001**				13.7636	6	**0.032**
Farmland	**Year**	7.1238	1	**0.008**	0.7292	1	0.393	181.7344	1	**<0.001**	13.8167	1	**<0.001**	215.6147	1	**<0.001**
	Region	2.4863	6	0.87	0.048	6	1	8.3942	6	0.211	5.9861	6	0.425	14.784	6	**0.022**
	Year: Region	66.372	6	**<0.001**	16.0037	6	0.014	12.7625	6	**0.047**	79.4729	6	**<0.001**	89.4334	6	**<0.001**
Urban	**Year**	3.5207	1	0.061	3.0796	1	0.079	134.4579	1	**<0.001**	3.209	1	0.073	704.3111	1	**<0.001**
	Region	0.0274	5	1	0.0342	5	1	2.1776	5	0.824	0.6693	5	0.985	7.8114	5	0.167
	Year: Region										22.3087	5	**<0.001**	94.1471	5	**<0.001**
Wetland	**Year**	2.596	1	0.107	0.2452	1	0.62	2.4368	1	0.119	10.9749	1	**0.001**	1.8434	1	0.175
	Region	0.0446	3	0.998	0.004	3	1	0.0347	3	0.998	0.2347	3	0.972	0.0262	3	0.999
	Year: Region				15.5484	3	**0.001**									
Semi-natural	**Year**	0.1208	1	0.728	2.2803	1	0.131	0.3527	1	0.553	13.0457	1	**<0.001**	0.7209	1	0.396
	Region	0.0162	6	1	0.0924	6	1	0.0159	6	1	2.2957	6	0.891	0.0398	6	1
	Year: Region							17.0422	6	**0.009**	23.2968	6	**0.001**			

Table A.4.9. Results for pairwise comparison of differences in temporal trends between each pair of regions for each habitat type and functional diversity index; functional richness (FRic), functional evenness (FEve), functional dispersion (FDis), functional originality (FOri) and functional specialisation (FSpe). Annual values for each index were standardised at the site-level prior to analyses. Significant values highlighted in bold.

		FRic			**FEve**			**FDis**			**FOri**			**FSpe**		
Habitat	**Pairwise comparison**	**Estimate (SE)**	**Z**	**p**	**Estimate (SE)**	**Z**	**p**	**Estimate (SE)**	**Z**	**p**	**Estimate (SE)**	**Z**	**p**	**Estimate (SE)**	**Z**	**p**
Forest	Central & East - East Med	-0.2848 (0.1842)	-1.5464	0.9349	-0.2969 (0.1843)	-1.6107	0.9076	-0.0946 (0.1842)	-0.5137	1				0.1494 (0.184)	0.8118	1
	Central & East - North	0.0018 (0.0038)	0.4553	1	0.0077 (0.0039)	1.9911	0.6318	0.0013 (0.0038)	0.3459	1				-0.0115 (0.0038)	-2.9962	0.0559
	Central & East - South	0.0153 (0.0044)	3.5103	**0.0094**	-0.0028 (0.0044)	-0.638	1	0.0099 (0.0044)	2.2608	0.3967				-0.0028 (0.0044)	-0.6502	1
	Central & East - Southeast	-0.031 (0.0246)	-1.2619	0.9923	-0.0059 (0.0246)	-0.2387	1	0.0332 (0.0246)	1.3504	0.9832				0.0178 (0.0246)	0.7254	1
	Central & East - West	0.0147 (0.0036)	4.0569	**0.001**	-0.0021 (0.0036)	-0.5874	1	0.0151 (0.0036)	4.1635	**<0.001**				-0.0079 (0.0036)	-2.1881	0.457
	Central & East - West Bal	-0.0885 (0.0948)	-0.9338	0.9999	-0.0577 (0.0948)	-0.6088	1	0.0612 (0.0948)	0.6457	1				-0.0828 (0.0947)	-0.875	1
	East Med - North	0.2866 (0.1842)	1.5561	0.9312	0.3046 (0.1843)	1.6525	0.8865	0.0959 (0.1842)	0.5209	1				-0.1609 (0.184)	-0.8745	1
	East Med - South	0.3001 (0.1842)	1.6294	0.8985	0.2941 (0.1843)	1.5956	0.9146	0.1045 (0.1842)	0.5672	1				-0.1522 (0.184)	-0.8271	1
	East Med - Southeast	0.2538 (0.1858)	1.3664	0.9809	0.291 (0.1859)	1.5656	0.9275	0.1278 (0.1858)	0.688	1				-0.1316 (0.1856)	-0.7089	1
	East Med - West	0.2996 (0.1842)	1.6265	0.9	0.2948 (0.1843)	1.5993	0.913	0.1097 (0.1842)	0.5958	1				-0.1573 (0.184)	-0.855	1
	East Med - West Bal	0.1964 (0.207)	0.9484	0.9999	0.2392 (0.2072)	1.1543	0.9975	0.1558 (0.207)	0.7525	1				-0.2322 (0.2068)	-1.1226	0.9983
	North - South	0.0135 (0.0037)	3.6776	**0.0049**	-0.0105 (0.0037)	-2.8354	0.0918	0.0085 (0.0037)	2.3134	0.3555				0.0087 (0.0037)	2.3598	0.3213
	North - Southeast	-0.0328 (0.0245)	-1.3387	0.9848	-0.0135 (0.0245)	-0.5527	1	0.0319 (0.0245)	1.3016	0.9889				0.0293 (0.0245)	1.1997	0.9959
	North - West	0.013 (0.0027)	4.7697	**<0.001**	-0.0098 (0.0027)	-3.6014	**0.0066**	0.0138 (0.0027)	5.0672	**<0.001**				0.0036 (0.0027)	1.3149	0.9876
	North - West Bal	-0.0902 (0.0947)	-0.9525	0.9998	-0.0654 (0.0948)	-0.6899	1	0.0599 (0.0947)	0.6319	1				-0.0713 (0.0946)	-0.7534	1
	South - Southeast	-0.0463 (0.0246)	-1.8856	0.7233	-0.0031 (0.0246)	-0.1257	1	0.0233 (0.0246)	0.9501	0.9998				0.0206 (0.0245)	0.8413	1
	South - West	-6e-04 (0.0034)	-0.1669	1	7e-04 (0.0034)	0.189	1	0.0053 (0.0034)	1.5287	0.9413				-0.0051 (0.0034)	-1.4853	0.9552
	South - West Bal	-0.1038 (0.0948)	-1.0953	0.9988	-0.0549 (0.0948)	-0.5795	1	0.0513 (0.0948)	0.5417	1				-0.08 (0.0947)	-0.845	1
	Southeast - West	0.0457 (0.0245)	1.8705	0.7358	0.0037 (0.0245)	0.1528	1	-0.0181 (0.0245)	-0.7391	1				-0.0258 (0.0244)	-1.0544	0.9993
	Southeast - West Bal	-0.0575 (0.0978)	-0.5877	1	-0.0519 (0.0978)	-0.5301	1	0.028 (0.0978)	0.2863	1				-0.1006 (0.0977)	-1.0304	0.9995
	West - West Bal	-0.1032 (0.0947)	-1.0896	0.9989	-0.0556 (0.0948)	-0.5865	1	0.0461 (0.0947)	0.4864	1				-0.0749 (0.0946)	-0.7913	1

Farmland	Central & East - East Med	-0.0437 (0.0209)	-2.0914	0.5419	0.0446 (0.0209)	2.1301	0.5075	0.0271 (0.0209)	1.2987	0.9892	0.0073 (0.0209)	0.3482	1	0.0195 (0.0208)	0.9347	0.9999
	Central & East - North	0.0046 (0.0054)	0.8548	1	0.0023 (0.0054)	0.4272	1	-0.0111 (0.0054)	-2.0674	0.5634	0.0012 (0.0054)	0.2155	1	0.0088 (0.0054)	1.6504	0.8876
	Central & East - South	0.0203 (0.0031)	6.5028	**<0.001**	-0.0032 (0.0031)	-1.017	0.9996	0.0034 (0.0031)	1.0961	0.9988	-0.0135 (0.0031)	-4.3215	**<0.001**	0.0063 (0.0031)	2.0232	0.6031
	Central & East - Southeast	0.0261 (0.0097)	2.6789	0.1442	-0.0131 (0.0098)	-1.3385	0.9848	0.0049 (0.0097)	0.5002	1	0.0293 (0.0097)	3.0009	0.055	0.0095 (0.0097)	0.9764	0.9998
	Central & East - West	0.0152 (0.0025)	6.177	**<0.001**	-0.006 (0.0025)	-2.4527	0.2591	3e-04 (0.0024)	0.1064	1	0.0032 (0.0025)	1.2863	0.9904	-0.011 (0.0024)	-4.5239	**<0.001**
	Central & East - West Bal	0.039 (0.0111)	3.5114	**0.0093**	-0.0114 (0.0111)	-1.0247	0.9995	0.0198 (0.0111)	1.7844	0.8026	0.0452 (0.0111)	4.0685	**0.001**	-0.0017 (0.0111)	-0.1567	1
	East Med - North	0.0483 (0.0213)	2.2635	0.3945	-0.0423 (0.0214)	-1.9788	0.6428	-0.0382 (0.0213)	-1.7926	0.7966	-0.0061 (0.0213)	-0.2867	1	-0.0106 (0.0213)	-0.5	1
	East Med - South	0.064 (0.0209)	3.0626	**0.0451**	-0.0478 (0.0209)	-2.2833	0.3788	-0.0237 (0.0209)	-1.1365	0.998	-0.0207 (0.0209)	-0.9929	0.9997	-0.0132 (0.0208)	-0.634	1
	East Med - Southeast	0.0698 (0.0228)	3.0605	**0.0454**	-0.0577 (0.0229)	-2.5227	0.2181	-0.0223 (0.0228)	-0.976	0.9998	0.022 (0.0228)	0.9635	0.9998	-0.01 (0.0227)	-0.4392	1
	East Med - West	0.0589 (0.0208)	2.8337	0.0923	-0.0506 (0.0208)	-2.4297	0.2737	-0.0269 (0.0208)	-1.2929	0.9898	-0.0041 (0.0208)	-0.1975	1	-0.0305 (0.0207)	-1.4716	0.959
	East Med - West Bal	0.0827 (0.0234)	3.5334	**0.0086**	-0.056 (0.0235)	-2.3871	0.3021	-0.0073 (0.0234)	-0.3138	1	0.0379 (0.0234)	1.62	0.9032	-0.0212 (0.0233)	-0.9086	0.9999
	North - South	0.0157 (0.0053)	2.9599	0.0627	-0.0055 (0.0053)	-1.0322	0.9995	0.0145 (0.0053)	2.7446	0.1198	-0.0146 (0.0053)	-2.7627	0.1137	-0.0026 (0.0053)	-0.486	1
	North - Southeast	0.0215 (0.0107)	2.0195	0.6065	-0.0154 (0.0107)	-1.4398	0.967	0.016 (0.0106)	1.5008	0.9505	0.0281 (0.0107)	2.6362	0.1621	6e-04 (0.0106)	0.0608	1
	North - West	0.0106 (0.0049)	2.1613	0.4801	-0.0083 (0.0049)	-1.6891	0.8658	0.0114 (0.0049)	2.3127	0.356	0.002 (0.0049)	0.4092	1	-0.0199 (0.0049)	-4.0554	**0.0011**
	North - West Bal	0.0344 (0.0119)	2.8881	0.0783	-0.0137 (0.0119)	-1.1481	0.9977	0.0309 (0.0119)	2.5973	0.1798	0.044 (0.0119)	3.6957	0.0046	-0.0106 (0.0119)	-0.8909	0.9999
	South - Southeast	0.0059 (0.0097)	0.604	1	-0.0099 (0.0097)	-1.0177	0.9996	0.0015 (0.0097)	0.1508	1	0.0427 (0.0097)	4.3978	**<0.001**	0.0032 (0.0097)	0.3316	1
	South - West	-0.005 (0.0023)	-2.2215	0.4288	-0.0028 (0.0023)	-1.2616	0.9923	-0.0031 (0.0022)	-1.4038	0.9745	0.0166 (0.0023)	7.3424	**<0.001**	-0.0173 (0.0022)	-7.7151	**<0.001**
	South - West Bal	0.0188 (0.0111)	1.692	0.8641	-0.0082 (0.0111)	-0.7413	1	0.0164 (0.0111)	1.4809	0.9564	0.0586 (0.0111)	5.2908	**<0.001**	-0.008 (0.011)	-0.7256	1
	Southeast - West	-0.0109 (0.0095)	-1.1438	0.9978	0.007 (0.0095)	0.7391	1	-0.0046 (0.0095)	-0.485	1	-0.0261 (0.0095)	-2.7381	0.122	-0.0205 (0.0095)	-2.1625	0.4791
	Southeast - West Bal	0.0129 (0.0144)	0.8959	0.9999	0.0017 (0.0144)	0.1159	1	0.0149 (0.0144)	1.0376	0.9994	0.0159 (0.0144)	1.1079	0.9986	-0.0112 (0.0143)	-0.7823	1
	West - West Bal	0.0238 (0.0109)	2.1789	0.4649	-0.0054 (0.0109)	-0.4922	1	0.0195 (0.0109)	1.7933	0.7961	0.042 (0.0109)	3.8496	**0.0025**	0.0093 (0.0109)	0.8554	1
Urban	Central & East - East Med										0.1277 (0.0899)	1.4201	0.9208	-0.1635 (0.0879)	-1.8596	0.6229
	Central & East - North										0.0115 (0.0122)	0.9411	0.9983	0.0055 (0.0119)	0.4659	1
	Central & East - South										-0.0041 (0.0086)	-0.4791	1	-0.014 (0.0084)	-1.6712	0.7751
	Central & East - Southeast										-0.0013 (0.0266)	-0.05	1	0.0302 (0.026)	1.1611	0.9854
	Central & East - West										0.0187 (0.0063)	2.9815	**0.0422**	-0.0428 (0.0061)	-7.0217	**<0.001**
	East Med - North										-0.1162 (0.0903)	-1.2867	0.9636	0.169 (0.0883)	1.9137	0.5764
	East Med - South										-0.1318 (0.0899)	-1.4658	0.9007	0.1495 (0.0879)	1.7004	0.7532
	East Med - Southeast										-0.129 (0.0934)	-1.382	0.9354	0.1936 (0.0913)	2.1213	0.4039

	East Med - West										-0.109 (0.0897)	-1.2144	0.978	0.1207 (0.0877)	1.3756	0.9377
	North - South										-0.0156 (0.0122)	-1.2744	0.9664	-0.0195 (0.0119)	-1.6378	0.799
	North - Southeast										-0.0128 (0.028)	-0.4563	1	0.0246 (0.0273)	0.9009	0.999
	North - West										0.0073 (0.0107)	0.6781	1	-0.0483 (0.0105)	-4.6241	**<0.001**
	South - Southeast										0.0028 (0.0266)	0.1044	1	0.0442 (0.026)	1.6985	0.7547
	South - West										0.0228 (0.0064)	3.5845	**0.0051**	-0.0288 (0.0061)	-4.6855	**<0.001**
	Southeast - West										0.02 (0.026)	0.7708	0.9998	-0.073 (0.0254)	-2.8773	0.0585
Wetland	Central & East - North				-0.0565 (0.0328)	-1.7246	0.4116									
	Central & East - South				-0.0988 (0.037)	-2.6678	**0.0449**									
	Central & East - West				-0.0752 (0.0324)	-2.3249	0.1146									
	North - South				-0.0423 (0.0191)	-2.2112	0.1516									
	North - West				-0.0188 (0.0065)	-2.8946	**0.0226**									
	South - West				0.0236 (0.0185)	1.2757	0.7419									
Semi-natural	Central & East - East Med							0.0226 (0.0476)	0.4758	1	0.0362 (0.0474)	0.7654	1			
	Central & East - North							0.0141 (0.0141)	1.004	0.9996	0.0123 (0.014)	0.8769	1			
	Central & East - South							0.0279 (0.0132)	2.1112	0.5243	0.0337 (0.0132)	2.558	0.1993			
	Central & East - Southeast							0.0607 (0.0481)	1.264	0.9922	0.0165 (0.0478)	0.345	1			
	Central & East - West							0.0327 (0.0125)	2.61	0.1739	0.0384 (0.0125)	3.0611	**0.0453**			
	Central & East - West Bal							-0.1191 (0.0794)	-1.499	0.9511	0.1428 (0.0791)	1.8061	0.7866			
	East Med - North							-0.0085 (0.0465)	-0.1828	1	-0.0239 (0.0463)	-0.5175	1			
	East Med - South							0.0052 (0.0462)	0.1136	1	-0.0025 (0.046)	-0.0551	1			
	East Med - Southeast							0.0381 (0.0653)	0.5833	1	-0.0197 (0.065)	-0.3036	1			
	East Med - West							0.0101 (0.046)	0.219	1	0.0021 (0.0458)	0.0459	1			
	East Med - West Bal							-0.1417 (0.0909)	-1.5584	0.9303	0.1066 (0.0905)	1.1773	0.9968			
	North - South							0.0137 (0.0083)	1.6516	0.887	0.0214 (0.0084)	2.5624	0.197			
	North - Southeast							0.0466 (0.047)	0.9924	0.9997	0.0042 (0.0468)	0.0897	1			
	North - West							0.0186 (0.0072)	2.5901	0.1833	0.026 (0.0072)	3.6157	**0.0063**			
	North - West Bal							-0.1332 (0.0788)	-1.6912	0.8645	0.1305 (0.0784)	1.6643	0.8801			
	South - Southeast							0.0329 (0.0467)	0.7036	1	-0.0172 (0.0465)	-0.37	1			

	South - West							0.0048 (0.0052)	0.9319	0.9999	0.0046 (0.0052)	0.8916	0.9999			
	South - West Bal							-0.147 (0.0786)	-1.8689	0.7371	0.1091 (0.0783)	1.3933	0.9765			
	Southeast - West							-0.028 (0.0465)	-0.6025	1	0.0218 (0.0463)	0.4716	1			
	Southeast - West Bal							-0.1798 (0.0912)	-1.9717	0.649	0.1263 (0.0908)	1.3912	0.9769			
	West - West Bal							-0.1518 (0.0785)	-1.9332	0.6828	0.1044 (0.0782)	1.336	0.9851			

Table A.4.10. Results of GLMMs of the association between site-level trends in functional diversity indices and site-level trends in total number of individuals and species in five broad habitat types across Europe.

		FRic				**FEve**				**FDis**				**FOri**				**FSpe**			
Habitat	**Fixed effects**	**Estimate (SE)**	**X^2**	**df**	**p**	**Estimate (SE)**	**X^2**	**df**	**p**	**Estimate (SE)**	**X^2**	**df**	**p**	**Estimate (SE)**	**X^2**	**df**	**p**	**Estimate (SE)**	**X^2**	**df**	**p**
Forest	**Species richness**	0.7406 (0.0122)	3669.3979	1	**<0.001**	0.0102 (0.0186)	0.3042	1	0.581	0.3203 (0.0184)	320.5183	1	**<0.001**	-0.0706 (0.0193)	11.3212	1	**0.001**	0.051 (0.0192)	7.0267	1	**0.008**
	Number of individuals	0.0179 (0.012)	2.2356	1	0.135	-0.2224 (0.0182)	148.6870	1	**<0.001**	-0.0815 (0.018)	21.1376	1	**<0.001**	0.0621 (0.0189)	10.5420	1	**0.001**	-0.0342 (0.0189)	3.2838	1	0.07
	Species richness: Number of individuals									0.1416 (0.0292)	23.5536	1	**<0.001**	0.0995 (0.0305)	10.6411	1	**0.001**				
Farmland	**Species richness**	0.7379 (0.0081)	8246.1018	1	**<0.001**	-0.0078 (0.0115)	0.9606	1	0.327	0.2229 (0.0123)	319.1175	1	**<0.001**	-0.065 (0.0122)	28.2138	1	**<0.001**	0.0074 (0.0124)	0.6386	1	0.424
	Number of individuals	0.0319 (0.0079)	16.2338	1	**<0.001**	-0.2846 (0.0112)	638.4518	1	**<0.001**	-0.1075 (0.012)	77.2615	1	**<0.001**	0.0953 (0.0119)	63.7625	1	**<0.001**	0.0112 (0.0121)	0.6270	1	0.428
	Species richness: Number of individuals					-0.0771 (0.018)	18.2495	1	**<0.001**	-0.0861 (0.0193)	19.8816	1	**<0.001**					0.0544 (0.0195)	7.7623	1	**0.005**
Urban	**Species richness**	0.7475	1343.8549	1	**<0.001**	0.0027	0.0649	1	0.799	0.2916	109.8201	1	**<0.001**	0.1205	16.8726	1	**<0.001**	0.0851	7.5553	1	**0.006**

		(0.0203)				(0.0267)				(0.0278)				(0.0293)				(0.0293)			
	Number of individuals	0.0132 (0.0189)	1.3474	1	0.246	-0.2545 (0.0248)	114.3495	1	**<0.001**	-0.2668 (0.0256)	108.5969	1	**<0.001**	0.0416 (0.027)	2.3749	1	0.123	-0.202 (0.0272)	51.7217	1	**<0.001**
	Species richness: Number of individuals	0.0914 (0.0315)	8.4426	1	**0.004**	-0.0817 (0.0414)	3.8969	1	**0.048**									0.0906 (0.0454)	3.9850	1	**0.046**
Wetland	**Species richness**	0.6634 (0.0297)	493.9431	1	**<0.001**	0.0355 (0.0444)	0.6381	1	0.424	0.1892 (0.0461)	18.8449	1	**<0.001**	-9e-04 (0.0489)	0.0105	1	0.918	-0.0602 (0.0478)	1.7596	1	0.185
	Number of individuals	0.12 (0.0289)	17.0056	1	**<0.001**	-0.3323 (0.0435)	58.3348	1	**<0.001**	-0.0483 (0.0451)	0.9893	1	0.32	-0.0227 (0.0475)	0.2561	1	0.613	0.0594 (0.0464)	1.5864	1	0.208
	Species richness: Number of individuals	0.1605 (0.0485)	10.9530	1	**0.001**					-0.4685 (0.0752)	38.8048	1	**<0.001**	0.2062 (0.0796)	6.7121	1	**0.01**	0.1623 (0.078)	4.3338	1	**0.037**
Semi-natural	**Species richness**	0.8081 (0.0217)	1389.6001	1	**<0.001**	0.1548 (0.0309)	25.4240	1	**<0.001**	0.3198 (0.0326)	97.1371	1	**<0.001**	-0.0232 (0.0342)	0.4621	1	0.497	0.0014 (0.0333)	0.0017	1	0.967
	Number of individuals	0.0601 (0.0198)	9.0543	1	**0.003**	-0.2794 (0.0281)	99.4123	1	**<0.001**	-0.2041 (0.0296)	47.8890	1	**<0.001**	0.0096 (0.0312)	0.0951	1	0.758	-0.0618 (0.0303)	4.1535	1	**0.042**
	Species richness: Number of individuals	-0.1227 (0.036)	11.6472	1	**0.001**	-0.1667 (0.0512)	10.6147	1	**0.001**	-0.2029 (0.054)	14.1348	1	**<0.001**								

Table A.4.11. Results of GLMMs of the temporal variation in species richness and total number of individuals for five broad habitat types in Europe between 1998 and 2017. Annual values for total number of species and individuals were both standardised at the site-level prior to analyses.

		Number of species				**Number of individuals**			
Habitat	**Fixed effects**	**Estimate (SE)**	**X^2**	**df**	**p**	**Estimate (SE)**	**X^2**	**df**	**p**
Forest	**Longitude**	0.0002414 (0.0007448)	0.1050648	1	0.746	0.000268 (0.000743)	0.1304682	1	0.718
	Latitude	0.0001623 (0.0010229)	0.0251882	1	0.874	0.0000191 (0.00102)	0.0003509	1	0.985
	Year	-0.0038226 (0.0030342)	1.5872668	1	0.208	-0.00436 (0.00384)	1.2884397	1	0.256
Farmland	**Longitude**	-0.0002139 (0.0004182)	0.261548	1	0.609	0.0001348 (0.0004183)	0.1039262	1	0.747
	Latitude	0.0003793 (0.0009395)	0.1629697	1	0.686	0.0000398 (0.0009396)	0.0017945	1	0.966
	Year	0.0029447 (0.002788)	1.1155618	1	0.291	-0.0019494 (0.0026092)	0.55823	1	0.455
Urban	**Longitude**	0.0001552 (0.0011328)	0.0187805	1	0.891	0.0006037 (0.0011305)	0.2851805	1	0.593
	Latitude	0.0001491 (0.0024416)	0.003729	1	0.951	0.0009466 (0.0024342)	0.1512083	1	0.697
	Year	-0.0028926 (0.0031322)	0.8528126	1	0.356	-0.0139776 (0.0040623)	11.8391433	1	**0.001**
Wetland	**Longitude**	0.0000197 (0.00156)	0.0001587	1	0.99	0.0001253 (0.0015365)	0.0066466	1	0.935

	Latitude	0.000378 (0.00324)	0.0136731	1	0.907	0.0008977 (0.0031895)	0.07921	1	0.778
	Year	-0.00588 (0.00243)	5.8692862	1	**0.015**	-0.0170702 (0.0027519)	38.4769749	1	<**0.001**
Semi-natural	**Longitude**	0.0006795 (0.0011696)	0.3375657	1	0.561	0.0012705 (0.0011614)	1.1966341	1	0.274
	Latitude	0.0002418 (0.0014576)	0.0275286	1	0.868	0.0006111 (0.0014508)	0.177436	1	0.674
	Year	-0.0086215 (0.0035737)	5.8200239	1	**0.016**	-0.0197463 (0.0053275)	13.738272	1	<**0.001**

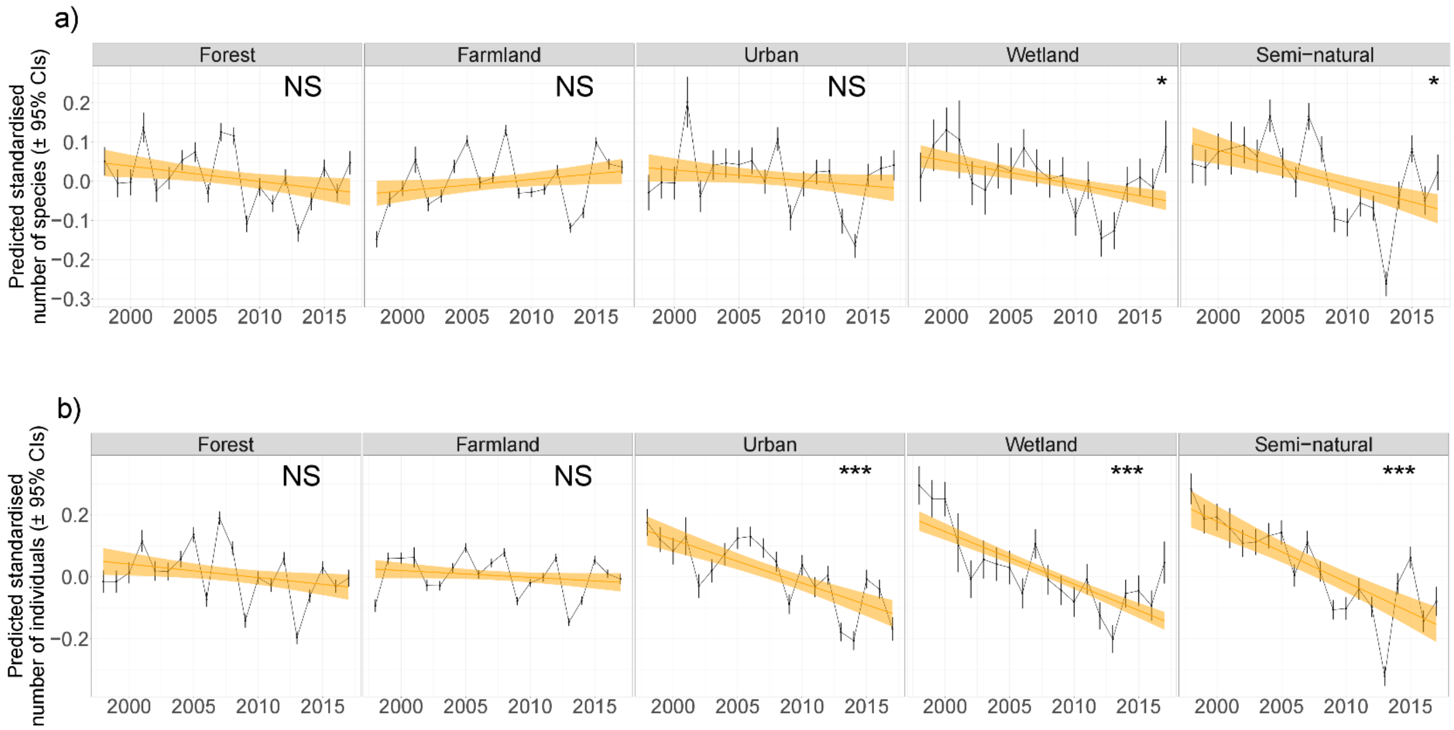


Fig. A.4.2. Predicted annual variation in a) total number of species and b) total number of individuals in five broad habitat types in Europe between 1998 and 2017. Annual values for total number of species and individuals in each habitat were standardised at the site-level prior to analyses. The orange line in each panel represents the predicted trend from GLMMs (with year as continuous variable) for each habitat, with shaded areas indicating 95% confidence intervals. Points in each panel represent the predicted annual values from the same GLMMs as above, but with year as categorical variable. Vertical lines either side of each point represent 95% confidence intervals. Significance of the predicted temporal trend from each GLMM with year as continuous variable are shown in the upper right corner of each panel; ***, $p < 0.001$, **, $p < 0.01$, *, $p < 0.05$, NS, not significant.

Chapter Five: Using temporal and spatial patterns in functional diversity of species subsets to describe patterns in the overall avian community

5.1 Abstract

Human-induced land use change impacts temporal and spatial patterns in species richness, relative abundances and community structure. As a result, ecological communities are shifting away from specialists and towards generalist species, and potentially habitat visitors *i.e.*, species which use habitats intermittently. This may cause increased functional homogenisation and have negative impacts on ecosystem service provision if communities become functionally more similar over time. The challenge of understanding these patterns is exacerbated by site-level differences in abiotic and biotic filters which influence the relative abundance, distribution of species and functional composition of communities. To understand patterns in community structure, we explore temporal changes in functional diversity for avian communities within forest and farmland habitat in Europe, as these habitats have experienced significant human modification in recent decades. We explore trends for the full avian community in both habitats and use patterns in species subsets; generalists, specialists and visitors to understand the mechanisms that may drive them. In addition, we examine patterns for species subsets using a null model approach whereby observed temporal and spatial functional richness were compared to those expected based on random simulated communities. We find that for the full avian community and species subsets, the occupied functional trait space remains stable or even increases, while species' abundances become more unevenly distributed over time. This suggests that during the timeframe of this study, ecosystem functionality is protected against changing environmental conditions by changes in the relative abundance of functionally similar species. In addition, we find that observed functional diversity in both habitats and all subset groups are lower than expected over time suggesting that environmental filtering is acting on community functional structure. Finally, results show that the extent to which abiotic and biotic filters shape the functional composition of communities varies across Europe. We recommend that functional diversity of generalists,

specialists and habitat visitors should be considered further within policy and land management in order to monitor more nuanced changes in community functional composition overall and to monitor potential changes in ecosystem functioning.

5.2 Introduction

Species richness, relative abundances and community structures are driven by interactions between broad scale processes such as abiotic environmental variables and historic biogeography, and local scale factors such as resource availability, habitat complexity and species interactions (Montaña *et al*., 2014; Méndez *et al*., 2018). Ongoing human-induced land use change, driven by land conversion (alteration of natural habitats for human use) and intensification (Laliberté *et al*., 2010) are impacting the strength at which these environmental filters influence community composition patterns (Lawton, 1999; Carr and Fahrig, 2001; Pereira *et al*., 2012; Díaz *et al*., 2019). This can lead to severe and negative effects on biodiversity and ecosystem stability over time (Baselga *et al*., 2015; Henckel *et al*., 2019; de Souza Leite *et al*., 2022). In addition, studies have shown that declines in the quality and quantity of natural habitat have led to a shift in community composition over time towards an increase in the number of habitat generalists *i.e.,* species capable of exploiting a range of resources and modified landscapes, and a decline in the diversity and abundance of specialist species *i.e.,* species that use a smaller number of resources and are sensitive to rapidly changing environments (Julliard *et al*., 2006; Smart *et al*., 2006; Devictor *et al*., 2008; Clavel *et al*., 2011; Ibarra and Martin, 2015). Furthermore, the replacement of specialists with generalists can induce functional homogenisation processes (McKinney and Lockwood, 1999; Clavel *et al*., 2011), whereby there is a decrease in functional diversity and an increase in the similarity of functional traits expressed by a given community (Devictor *et al*., 2008; Clavel *et al*., 2011).

Functional diversity (hereafter FD) describes functional differences among species in a community by quantifying the range, distribution and abundance of their functional traits (morphological, physiological, phenological or behavioural) (Díaz and Cabido, 2001; Loreau, 2001; Hooper *et al.*, 2005). FD relates to the range of functional roles filled by species in a given community and can infer the scale of niche separation and resource use complementarity among species in that community (Petchey *et al.*, 2004). In this way, greater community FD infers greater ecosystem service provision (*e.g.*, pest control, pollination, soil quality) as species in the community fulfil a wider range of functional roles and occupy a greater array of ecological niches (Díaz and Cabido, 2001; Mason *et al.*, 2005). In contrast to this, a decline in FD for a given community suggests a disruption to service provision, as unique functional traits and niche space are lost from the community (Clavel *et al.*, 2011; Luck *et al.*, 2013). This relationship between FD and ecosystem function is also likely to exist at larger spatial scales *i.e.*, across countries and regions. For example, a gradient from low to high land-use intensification driven by differences in management practices or policies across spatial scales will cause FD to decrease in the same direction, leading to declines in ecosystem functioning (Flynn *et al.*, 2009; Laliberté *et al.*, 2010). Furthermore, spatial differences in environmental filters such as land use type (Luck *et al.*, 2013), habitat degradation (Jetz *et al.*, 2014; Fusco *et al.*, 2021), and fragmentation (Sonnier *et al.*, 2014) and climate (Díaz and Cabido, 2001) differ significantly across spatial scales, which in turn causes spatial differences in functional trait structures of ecological communities (de Bello *et al.*, 2013).

Species richness, a more common measure for the impact of human activity on biodiversity (Flynn *et al.*, 2009; Cadotte and Davies, 2010; Batáry *et al.*, 2015; Redhead *et al.*, 2018) and FD are often closely related, except in response to environmental changes (Flynn *et al.*, 2009; Guerrero *et al.*, 2014; Tarjuelo *et al.*, 2021). For example, high species richness but low FD suggests that the community is functionally redundant as a number of species are overlapping in their functional traits (Díaz and Cabido, 2001). FD may also experience steeper declines than species richness when functional redundancy is low to begin with *i.e.*, the number of species sharing similar traits is low. In addition, FD may decrease while species richness remains unchanged over time if the community experiences species turnover towards species that carry out similar functions, but have less unique functional traits compared to those species lost from the community (Mayfield *et al*., 2010; Ali *et al*., 2022). The relationship between FD and species richness has been extensively studied at fine spatial scales. However, information on temporal and spatial patterns in FD at continental or global scales is relatively limited (Tsianou and Kallimanis, 2016). In order to more closely monitor changes in global biodiversity and habitat quality, studies suggest that conservation management should consider FD over time and space in order to provide a more mechanistic understanding of the ecological impact of extinctions (Cadotte *et al*., 2011; Ali *et al*., 2022), to increase the effectiveness of management strategies (Wiens *et al*., 2008; Jetz *et al*., 2014; Morelli *et al*., 2017, 2021) and safeguard ecosystem service provision (Díaz *et al*., 2007).

In this study, we explore temporal and spatial patterns in FD for avian communities across Europe within forest and farmland, as these habitats have experienced significant changes in both land use and management in recent decades (McElhinny *et al*., 2005; Tscharntke *et al*., 2005). Birds are extensively used in FD studies as they are reliable indicators of ecosystem function due to their sensitivity to habitat change (Gregory, 2006). In addition, they provide a large range of ecosystem services such as seed dispersal (Stewart *et al*., 2020), scavenging (Luck *et al*., 2013), pest control (Pigot *et al*., 2020; Sekercioglu, 2006) and cultural and aesthetic services within art, religion and ecotourism (Sekercioglu, 2002). In addition, trait data which contributes to calculating FD is widely available for many avian species, allowing a detailed description of each species functional role to be built (Tobias *et al*., 2022).

We first explore temporal trends in FD indices for the full avian community in forest and farmland habitat and use patterns in species subsets; generalists, specialists and visitors in these habitats to understand overall trends further. Visitors to forest or farmland are defined as species which only use these habitats intermittently and do not show a preference for forest or farmland. Visitors are included in this study as increased habitat heterogeneity or fragmentation causes spill-over of species from other habitats as environmental conditions become more suitable for their survival (Jones *et al*., 2005). We then explore the impact of environmental filtering on temporal and spatial patterns in FD for species subsets in forest and farmland by comparing observed FD to expected values based on a null model approach, with species richness kept constant. By comparing observed temporal and spatial patterns in FD to null expectations based on species richness, we can explore assembly processes that may be acting on communities, giving us greater insight into the mechanisms that shape ecological communities overall (Petchey *et al*., 2007).

5.3 Methods

5.3.1 Bird and habitat data

Annual, site-level count data for 448 European breeding bird species were acquired from the Pan-European Common Bird Monitoring Scheme (PECBMS), who collate bird count data from national- level monitoring schemes. Site-level data from 1998 to 2017 for 22 countries were used to ensure coverage from a representative suite of countries. Each site was surveyed using one of three sampling techniques; point count, line transect or territory mapping (Brlík *et al.,* 2021), with survey technique varying with scheme. 35 subspecies were grouped at species level (Handbook of the Birds of the World and BirdLife International, 2020), leaving a total of 413 species.

Using the known geographic coordinates of the centroid for each site (21,551 in total), level three habitat data from Corine Land Cover (CLC) 2012 (Copernicus Land Monitoring Service, 2012) were extracted for 1km^2 areas centred on each site. Sites containing lagoons, estuaries and/or sea/ocean habitat were removed (687 sites) as open/marine habitat was not the focus of this study. For the remaining sites, level three CLC habitats present at each site were aggregated into five broad habitat types; forest, farmland, urban, wetland and semi-natural (Table A.5.1). The area of each habitat in each site was calculated and each site was defined according to the habitat which covered the largest area. In this study, we chose to focus on exploring temporal and spatial patterns in FD within forest and farmland. Therefore, the following steps were taken to calculate FD for sites dominated by either of these habitats.

5.3.2 Trait data

All subsequent analyses were carried out in R version 4.0.1 (R Core Team, 2020).

For our estimates of FD in avian communities across Europe, we compiled a suite of 15 traits (Altamirano *et al.*, 2020; Jacoboski and Hartz, 2020; Stewart *et al.*, 2020; Anderle *et al.*, 2022) which reflect diversity in avian species morphology, trophic niche position, diet, reproductive success, dispersal capabilities and evolutionary distinctness (Jetz *et al.*, 2014; Storchová and Hořák, 2018; Tobias *et al.*, 2022) (Table A.5.2). The matrix was supplemented with six further traits, derived from the Relative Habitat Use (RHU) metric (Larsen *et al.*, 2011) which describe the extent of each species' association with each of the five habitats (forest, farmland, urban, wetland and semi-natural) and degree of habitat specialisation (O'Reilly *et al.*, 2022). Due to data availability it was not possible to calculate RHUs for any of the five habitats for 153 out of the 413 species. These 153 species were removed from the trait matrix as suggested by other studies (Magneville *et al.*, 2022) as, although methods are in place to account for missing traits (see Gower, 1971), FD indices can be sensitive to the completeness of a community trait matrix, especially if a large proportion of species have missing traits (Májeková *et al*., 2016). Count data from sites within years in which these 153 species occurred were also removed. Following this, sites with fewer than three years of count data were removed. This left 260 species in the trait matrix and 15,085 sites.

5.3.3 Functional diversity

Prior to calculating FD indices, all continuous traits were log-transformed to ensure they were normally distributed (de Bello *et al*., 2021). First, a Gower species distance matrix was computed which gives trait-based distances between each pair of species, taking both continuous and categorical traits into consideration (Gower, 1971). Next, a Principal Coordinates Analysis (PCoA) was performed to ordinate species along major axes and plot them within multidimensional functional trait space, with each trait weighted equally. The quality.fspaces function from the mFD package version 1.0.0 (Magneville *et al*., 2022) was then used to evaluate the quality of the multidimensional space built by the PCoAs according to the deviation between trait-based distances and distances in functional space. From this, seven PCoA axes were identified as the optimum number to use which would ensure that trait-based distances between species were accurately represented, whilst allowing computation of FD indices (Magneville *et al*., 2022). Convex-hull based indices require a functional trait space with less axes than the number of species, therefore in order for FD indices to be calculated for a given site, species richness had to be >7 in a given year and must have met this requirement in ≥3 years. Sites which met this requirement (11,168) but had a species richness of ≤7 in a given year were assigned values of NA for each FD index in that year. For sites and years which met the species richness requirement, we used the mFD package (Magneville *et al*., 2022) to calculate annual FD indices; richness (FRic), evenness (FEve), dispersion (FDis), originality (FOri) and specialisation (FSpe) in order to gain an understanding of overall FD

(Mason *et al.*, 2005; Mouchet *et al.*, 2010) as each of these indices describe slightly different aspects of FD (Table A.5.3).

5.3.3.1 Functional diversity for habitat generalists, specialists and visitors

For sites and years which met the above species richness requirement, we also calculated FD indices for species subsets; forest generalists, specialists and visitors in sites dominated by forest, and farmland generalists, specialists and visitors for sites dominated by farmland. Species were defined as generalists, specialists or visitors to forest and farmland based on previously calculated RHU results (section 5.3.2.) which identified each species' degree of habitat specialisation. Species with a mean RHU ≥1 for forest or farmland only were defined as forest or farmland specialists respectively, and species with a mean RHU ≥1 for forest or farmland and at least one other habitat were defined as forest or farmland generalists respectively. Species which had a mean RHU <1 for forest or farmland (*i.e.,* no association) were defined as visitors of forest or farmland respectively.

For each species subset in turn (generalists, specialists, visitors), we used the process described in section 5.3.2. above to calculate FD indices. For generalists, specialists and visitors, the optimum number of PCoA axes were identified as six, five and seven respectively. Therefore, FD indices for a given site and year were calculated if species richness was greater than the number of axes for the respective subset. If species richness was equal to or below the number of axes in a given site and year for a subset group, values of NA were assigned to each FD index in that year for that subset.

5.3.4 Null models

FD and species richness are generally positively correlated, as the addition of a new species to a community causes FD to increase or stay the same (Petchey and Gaston, 2002). We therefore also used a simulation approach to calculate FD for species subsets in forest and farmland and compared observed values of FD to those expected from simulated null models. Null models were produced for each site and year by randomly selecting species from the regional pool, keeping species richness in that site and year constant. Two separate pools were used - one for forest, with all species recorded in sites defined as forest, and one for farmland, with all species recorded in sites defined as farmland. Studies at smaller, more local scales that compare observed FD to expected FD based on null models often account for spatial differences in habitat in order to understand biotic interactions (de Bello *et al.*, 2012; Laliberté *et al.*, 2013). However, at broader spatial scales, habitat filtering is likely to have a larger impact than biotic interactions (Díaz *et al.*, 1999; Chalmandrier *et al.*, 2013). Therefore, defining the regional species pool based on all species recorded in a given habitat across Europe allows us to explore spatial patterns in the intensity of environmental filtering, and its impact on community composition and FD. In addition, species were randomly chosen from the regional pool based on the proportion of sites they were recorded in, in a given year. This ensured that rarer species did not have a disproportionate effect on community composition (Mendez *et al.*, 2012). Furthermore, species' abundances were also randomly assigned based on the proportion of sites in which they had an abundance greater than the overall median across all species, sites and years in a given habitat. The range of abundances for species in forest and farmland were large (1 – 2289 and 1 – 2840 respectively), with 99.9% of species' abundances skewed towards lower abundances. However, species with large abundances in a given site can have a significant effect on FD indices which take abundances into consideration. The median abundance was therefore used as a reference as the median is more appropriate than the mean for highly skewed data. Therefore, species with no abundances greater than the median were randomly assigned abundances between the minimum and median. All other species were randomly assigned an abundance between the minimum and the maximum based on the proportion of their abundances greater than the median. For each site and year, 100 random communities were simulated and FD indices were calculated for generalists, specialists and visitors for forest and farmland habitats. Here, we focused on FRic as we found that it was the most highly correlated with species richness.

5.3.5 Statistical analysis

5.3.5.1 Temporal trends for the full avian community and species subsets

First, we explored pan-European temporal trends in FD indices for the full avian community in forest and farmland and then used trends for species subsets; generalists, specialists and visitors to explain the overall avian community trends. For this, FD indices for the full avian community and each species subset were first standardised at the site level by subtracting the mean site-level index from the annual index value and dividing by the site-level standard deviation. This allowed sites to be directly comparable as it accounts for potential differences in detectability, observer effects and differences in sampling protocol across survey schemes (Morrison *et al.*, 2021). To explore large-scale temporal trends in FD, separate general linear mixed models (GLMMs) were built for each FD index for the full avian community and for each of the species subsets in turn using the lme4 R package (Bates *et al.*, 2015). Standardised annual site-level values for the given FD index were used as the response variable and latitude, longitude and year (continuous) as fixed effects. Latitude and longitude were included to account for geographic differences in FD. Site, year and country were included as random effects, as avian communities across sites and years were not independent of one another. A likelihood ratio test carried out on the model identified the importance of each fixed effect by comparing models with all fixed effects included to those without each fixed term in turn. A study by Morrison *et al.,* (2021) which also uses the same PECBMS count data tested for spatial autocorrelation of modelled residuals, separately for each year, using Moran’s I. Although the study found significant spatial autocorrelation, the size of the estimates were minor and therefore were ignored. As the data used in Morrison *et al.*, (2021) and in this study are extremely similar, we also chose to ignore spatial autocorrelation issues in this study.

We then compared pan-European temporal trends between the full avian community and each of the species subsets for each habitat and index. For this, separate GLMMs were built for each index and habitat, using the same model structure as above with the addition of species group (full avian community, generalists, specialists, visitors) and interaction between species group and year (continuous) as fixed effects. A likelihood ratio test applied to the model identified the importance of each fixed effect. We explored the difference in temporal trends between each pair of species groups to determine if there were significant differences between them using the posthoc_Trends_Pairwise test from the grafify R package (Shenoy, 2021).

5.3.5.2 Species subsets: Expected vs. Observed

5.3.5.2.1 Temporal trends

To investigate community assembly patterns within each species subset, we compared temporal patterns of observed FRic with expected FRic of random communities. We used the standardised effect size index (SES) (Gotelli and McCabe, 2002; Mendez *et al*., 2012) to compare between observed and expected FRic and to explore the change in SES over time. For each species subset in turn, we calculated SES FRic for each year within each site as observed unstandardised FRic minus mean expected unstandardised FRic (mean calculated across 100 simulated communities)/ standard deviation of expected unstandardised FRic. A value greater than 0 infers that trait divergence/complementarity has occurred due to interspecific competition, and a value below 0 infers that trait convergence/similarity has occurred due to environmental filtering limiting the diversity of species in a habitat (Mendez *et al*., 2012). We then used separate GLMMs for each species subset with SES FRic as the response variable and latitude, longitude and year (continuous) as fixed effects. Latitude and longitude were included to account for any geographic differences in the SES FRic. Site, year and country were included as random effects. A likelihood ratio test identified the importance of each fixed effect.

5.3.5.2.2 Spatial patterns

Finally, to determine the effect of filtering processes on community structure across latitudinal and longitudinal gradients, we built separate GLMMs for each species subset within forest and farmland habitat in turn and used the SES FRic index as the response variable with latitude, longitude, year (continuous) and interactions between latitude and year and longitude and year as fixed effects with country included as a random effect. A likelihood ratio test identified the importance of each fixed effect.

5.4 Results

5.4.1 Temporal trends

In forest habitat, FEve increases and FDis decreases over time for the full avian community. However, FRic and FEve trends for forest specialists were more positive than the full community, generalists and visitors. In addition, FOri for forest generalists was more negative than the full community, specialists and visitors. Finally, FSpe for visitors was more positive than the full community, generalists and specialists (Fig. 5.1, Table A.5.4 – A.5.7). In farmland, FRic, FDis and FSpe increase over time for the full avian community. Additionally, FRic, FEve, FDis and FSpe for the full community were more positive than farmland generalists, specialists and visitors. By contrast FOri for the full community was more negative than generalists. FRic, FEve and FDis for farmland generalists were more negative than specialists and visitors but FOri and FSpe for generalists were more positive than specialists and visitors. Finally, FDis and FSpe for farmland specialists were more positive than visitors yet FSpe for specialists was more negative than visitors.

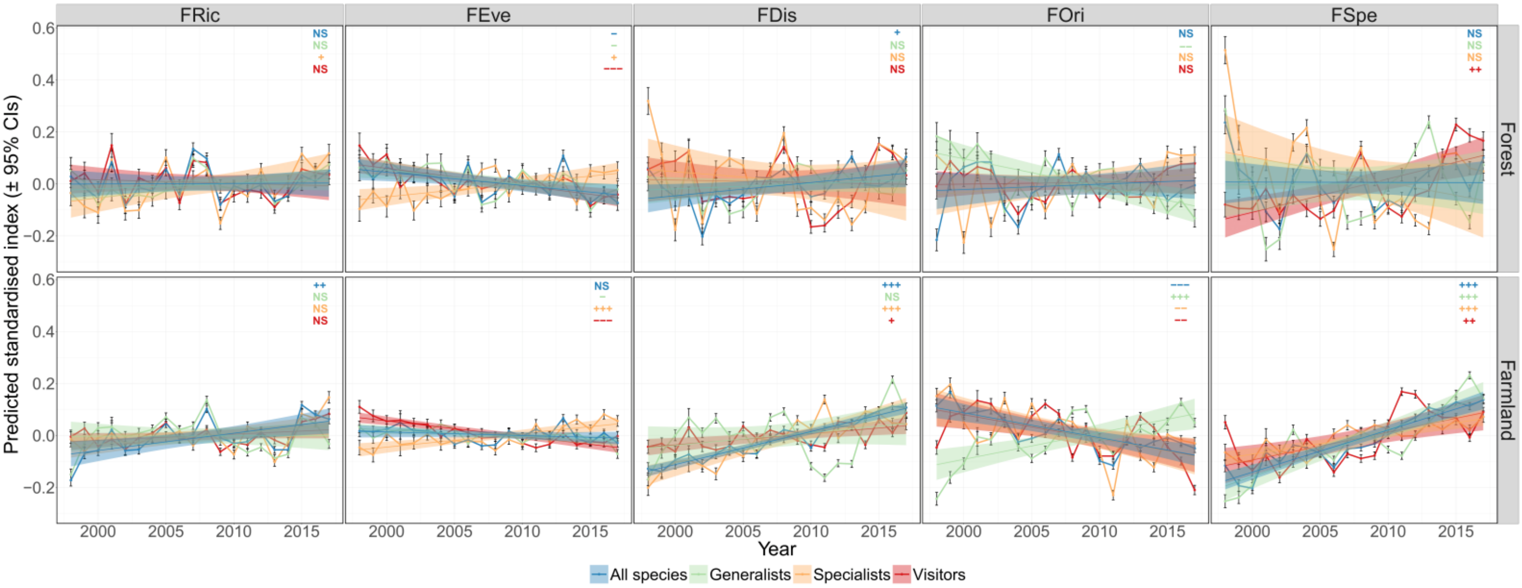


Fig. 5.1. Comparison of predicted European annual variation in functional diversity indices; richness (FRic), evenness (FEve), dispersion (FDis), originality (FOri) and specialisation (FSpe) between the full avian community in forest and farmland habitats and subsets of these communities; forest generalists, specialists and visitors, and farmland generalists, specialists and visitors respectively. Annual values for each index, habitat and species group were standardised at the site-level prior to analyses. Lines are coloured based on the species group with the solid straight line in each case representing the predicted trend from GLMMs (with year as continuous variable) for each index with shaded areas indicating 95% confidence intervals. Points in each panel for each species group represent the mean annual values for the given index, with vertical lines either side of the points representing standard error for that index and species group in that year. Significance of each trend for each species group is provided in the upper right corner of each plot; + (positive trend with p<0.05), ++ (positive trend with p<0.01), +++ (positive trend with p<0.001), - (negative trend with p<0.05), -- (negative trend with p<0.01), --- (negative trend with p<0.001), N.S. (not significant).

5.4.2 Observed vs. Expected

5.4.2.1 Temporal trends

SES FRic was less than 0 in all habitats and across all species subsets (Fig. 5.2). In forest habitat, SES FRic for specialists decreases over time. In addition, in farmland habitat, SES FRic for generalists increases over time, while it decreases for visitors (Table A.5.9).

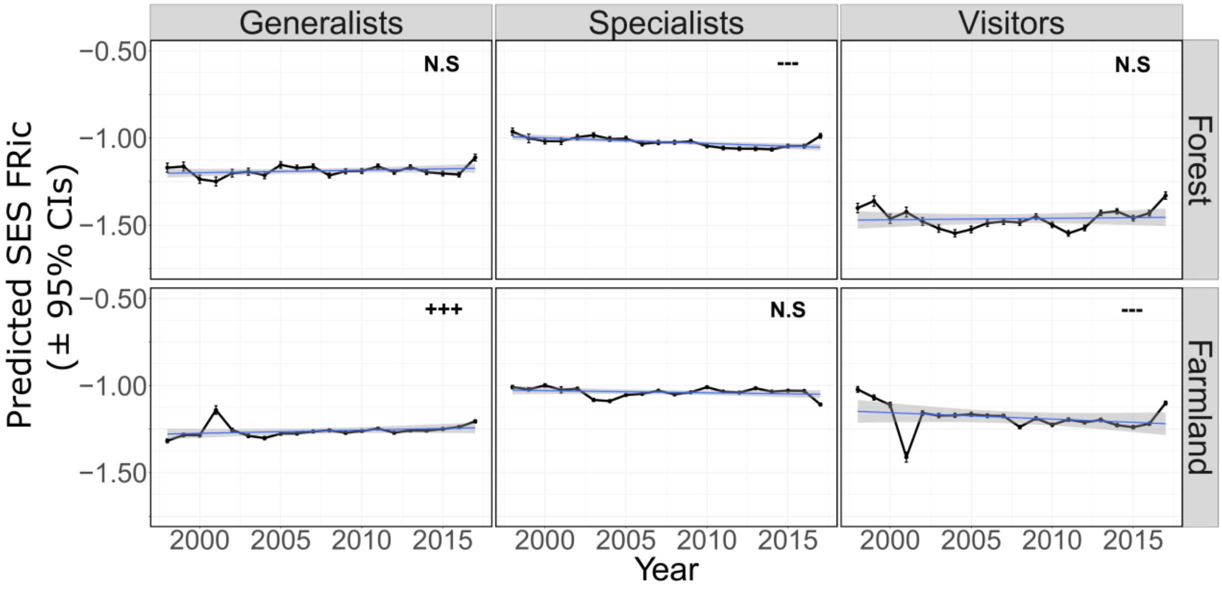
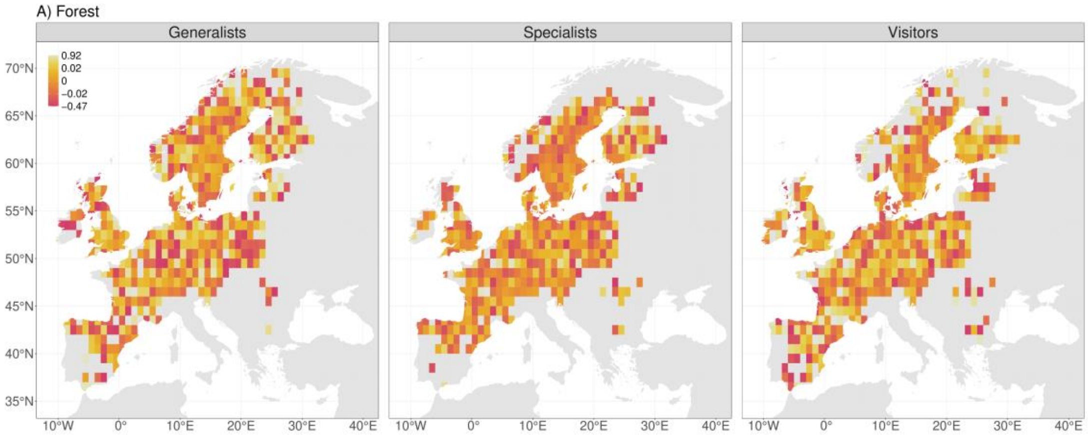


Fig. 5.2. Temporal trends in the standardised effect size (SES) of functional richness in forest and farmland habitat in Europe between 1998 to 2017 for generalists, specialists and visitors. Standardised effect size of FRic in each habitat for each of the three species groups were calculated as observed FRic minus mean expected FRic (mean calculated across 100 simulated communities)/ standard deviation of expected FRic. Solid straight line in each case represents the predicted trend from GLMMs (with year as continuous variable) for FRic with shaded areas indicating 95% confidence intervals. Points in each panel for each species group represent the mean annual values for FRic, with vertical lines either side of the points representing standard error and species group in that year. Significance of each trend for each species group is provided in the upper right corner of each plot; +++ (positive trend with p<0.001), --- (negative trend with p<0.001), N.S (not significant).

5.4.2.2 Spatial variation

SES FRic varied across the European landmass with the extent of this variation differing between species subset (Fig. 5.3). In forest, SES FRic for visitors was more positive in the North and West and more negative in the South and East (Table A. 5.10). In farmland, SES FRic for specialists and visitors were more negative in the North than in the South. By contrast, SES FRic for generalists was more positive in the North than in the South.

A) Forest



B) Farmland

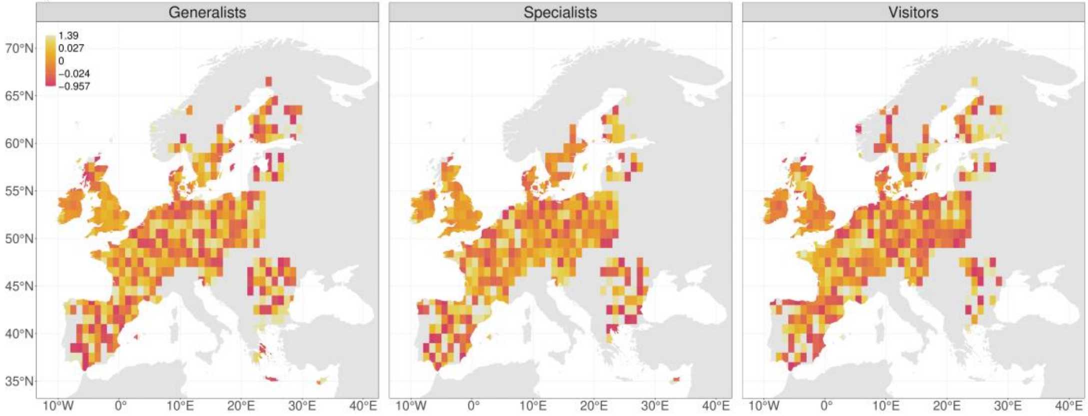


Fig. 5.3. Mean site-level trends in standardised effect size (SES) of functional richness in 1° x 1° grid squares across forest and farmland in Europe between 1998 and 2017 for generalists, specialists and visitors of each habitat. Standardised effect size of functional richness in each habitat for each of the three species groups were calculated as observed index value minus mean expected index value (mean calculated across 100 simulated communities)/ standard deviation of expected index value.

5.5 Discussion

Our study finds that within both forest and farmland habitats, functional diversity of avian communities has changed significantly over the past two decades, with these changes reflected in subset communities; generalists, specialists and visitors. However, the rate of change in functional diversity indices differs between subsets and according to habitat. A priori expectations were that avian communities would become more functionally homogenous as large-scale land-use change and habitat degradation continue. However, results show that in both habitats within the timeframe of this study, overall functional diversity remains stable, suggesting that ecosystem service provision is not affected by these anthropogenic activities. Conversely, results show that species' abundances are becoming more unevenly distributed over time for the full avian community and species subsets, suggesting that although ecosystem service provision is not affected by land-use changes, the species fulfilling those ecosystem services may be changing over time. In addition, negative values for the difference between observed and expected functional richness suggest that environmental filtering shapes community structure of species subsets, yet differences in the slope of these trends show that the strength of filtering processes impacts subset groups differently temporally and spatially.

5.5.1 Temporal and spatial patterns in forest habitat

FD results for avian communities overall show that although the occupied functional space has not changed, species' abundances have become more unevenly distributed over time and species far from the centroid (functionally distinct) show higher abundances than those close to the centroid (functionally similar). These overall patterns may be driven by generalists and visitors as we find that species' abundances within these subsets are also becoming more unevenly distributed over time. Abandonment of agricultural lands (García-Navas and Thuiller, 2020; Rey Benayas, 2007) and creation of woodlands in urban environments (Buron *et al*., 2022) increase vegetation and tree cover in these habitats. This may increase opportunities for some forest dwelling species to exploit resources in other habitats (Buron *et al*., 2022). As forest generalists are more likely than specialists to move into these habitats (Evans *et al*., 2018), the abundance of generalists in forest is likely to decline as a result. However, no overall change in generalist species richness, total abundance (Fig. A.5.1, Table A.5.8) or FRic, but a significant decrease in FOri shows that the difference in abundance between functionally similar generalist species is increasing over time. This suggests that generalist species moving into other habitats are maintained in forest, but at low numbers. With greater niche space now available for functionally similar generalist species, abundances of these generalists have the capacity to increase over time. This process highlights two points; first, although species can be defined as generalists, the extent to which each generalist species can utilise other habitats varies between them. This supports studies by others who highlight that habitat specialisation is more accurately defined along a continuous gradient of specialist to generalist rather than categorical classifications, with differences in the extent of specialism and generalism between individual species (Julliard *et al*., 2006; Reif *et al*., 2008; Devictor *et al*., 2008; Larsen *et al*., 2011; O'Reilly *et al*., 2022). Second, ecosystem functionality is protected by biodiversity against environmental changes as FRic is maintained while indices considering species' abundances show changes over time. This "insurance hypothesis" finds that high functional redundancy *i.e.,* significant overlap of functional traits, among species will ensure that available niche space will remain filled by back-up species if other species fail to fill that niche (Yachi and Loreau, 1999; Wittebolle *et al*., 2009). In addition to an uneven distribution of forest visitor species' abundances, we also find that functionally unique species are overall more abundant than functionally similar species. Forest area has increased in Europe in recent decades (Schelhaas *et al*., 2003; Palmero-Iniesta *et al*., 2021) with significant changes to its composition due to changes in management practices (McElhinny *et al*., 2005). These changes may not support a large diversity or abundance of forest visitors who will most likely prefer more open and fragmented habitat types (Menke *et al.*, 2012).

Within trends for the full avian community, patterns for forest specialists are masked by changes in forest generalists and visitors. We find that FRic of forest specialists increases and that species' abundances are more evenly distributed in functional trait space over time. These patterns are not reflected by the overall community, demonstrating how important changes in community structure can go undetected when FD of only the full avian community is explored. Improved FD for forest specialists may be due to an increase in forest cover in Europe (Forest Europe, 2020) which creates improved conditions and larger expanses of available habitat and niche space for forest specialists.

Overall negative values for SES FRic in all three subsets in forest suggest that environmental filtering is acting upon community assembly, limiting the range of species capable of exploiting forest resources. In addition, SES FRic for forest specialists becomes more negative over time, suggesting that forest conditions may be limiting the range of specialists over time. Studies suggest that dense forest canopy structures can limit species richness and functional richness (Gil-Tena *et al.*, 2007), while in other areas, habitat fragmentation can act as a filter to the range of species capable of utilising forest habitat (Terraube *et al.*, 2016). Therefore, temporal changes in management practices and land-use which impact total forest area in Europe may limit the range of species in forest than is expected by chance. Finally, we find that there is large spatial variation in the difference between observed and expected FRic in forest, suggesting that site-level abiotic and biotic factors affect the strength of filtering processes on community assembly (Mikusiński *et al.*, 2018).

5.5.2 Temporal and spatial patterns in farmland habitat

FD results for the full avian community show that the overall occupied functional space is increasing, with functionally distinct species having higher abundances than functionally similar species overall. However, results also show that differences in abundance between functionally similar species are increasing over time and/or that communities are becoming functionally more similar. These overall patterns may be driven by farmland specialists and visitors who also show similar changes but differ in that they do not show a change in total occupied functional trait space.

Increased agricultural intensification in recent decades has led to habitat simplification through monocrop expansion and removal of hedgerows and tree lines. This homogenization of farmland habitat structure has negatively impacted farmland specialists (Julliard *et al*., 2006; García-Navas and Thuiller, 2020) and supplementary analysis from this study finds similar results, with significant declines in the total abundance of farmland specialists (Fig. A.5.1, Table A.5.8). However results for farmland specialists in this study and findings by others (Voříšek *et al*., 2010) suggest that the most abundant or most common specialists have declined, or have been lost from farmland avian communities over time. This has resulted in a more even distribution of species' abundances overall, with functionally unique species having higher abundances relative to very low abundances of functionally similar species. In addition, results show that specialist communities are becoming more functionally similar, suggesting that environmental conditions and management strategies may be negatively impacting farmland specialists that fill specific niche spaces (Benton *et al*., 2003). Farmland visitors show similar trends to specialists, however, declines in FEve suggest that increased homogenisation of farmland landscapes may fail to support even abundances of visitor species as conditions will favour some species more than others. In contrast to these patterns, FD for farmland generalists show that species' distances to their nearest neighbour in functional trait space are increasing over time. This suggests that niche partitioning may cause species to become more distinct from one another over time (McGill *et al*., 2006).

Similar to forest, FD results for farmland show that ecosystem functioning is stable and maintained by species in avian communities, despite farmland habitats experiencing significant land-use changes and degradation in recent decades. However, this stability may be compromised during environmental changes if abundances are highly skewed towards few species in a community. For example, ecosystem functions carried out by highly abundant species may be lost if environmental conditions cause these species to decline or become extinct if no other species exist in the community to fulfil that function (Balvanera *et al*., 2005; Wittebolle *et al*., 2009).

SES FRic results for farmland suggest that ongoing environmental changes may limit the range of farmland visitors capable of using farmland resources. Furthermore, increase in farmland generalist SES FRic over time suggests that ongoing homogenisation of the farmland landscape and intensive management practices may increase the range of generalists in farmland habitat. Finally, we find significant spatial variation in the difference between observed and expected FRic in farmland habitat across Europe. This suggests that site-level factors such as environmental conditions, agricultural management or climate could all play significant roles in shaping the functional structure of overall avian communities and generalists, specialists and visitors within these communities (Kleijn and Sutherland, 2003; Concepción and Díaz, 2011; Mendez *et al*., 2012; Jerrentrup *et al*., 2017).

5.6 Conclusion

In this study we find that FD patterns for the overall avian community within forest and farmland are reflected within FD of generalists, specialists and visitors, with the extent of this relationship dependent on the species subset, FD index and habitat. We hypothesised that given ongoing harmful human activities causing significant land-use changes and habitat degradation, FD of generalists (and to a lesser extent visitors) would increase and specialists would decrease. However results show that FD remains stable or even increases over time for the full avian community in both habitats, but indices which consider species' abundances show larger changes over time. This suggests that within the timeframe of this study, ecosystem functionality is protected against changing environmental conditions by changes in the relative abundance of functionally similar generalist, specialist and/or visitor species. However, if highly abundant species which carry out specific ecosystem functions are lost from the community due to environmental changes, it may have a significant impact on ecosystem functioning if a functionally similar species is not available to fill that niche. This study suggests that conservation policy and management strategies should endeavour to maintain highly functionally diverse communities, where species' abundances are relatively even in functional trait space to ensure greater functional stability during environmental changes.

5.7 Appendices

Table A.5.1. Corine Land Cover 2012 Levels 1 – 3 with habitat category assigned to each Level 3 habitat

Assigned habitat category	Level 1	Level 2	Level 3
Urban	Artificial surfaces	Urban fabric	Continuous urban fabric
			Discontinuous urban fabric
		Industrial, commercial and transport units	Industrial or commercial units
			Road and rail networks and associated land
			Port areas
			Airports
		Mine, dump and construction sites	Mineral extraction sites
			Dump sites
			Construction sites
		Artificial, non-agricultural vegetated areas	Green urban areas
			Sport and leisure facilities
Farmland	Agricultural areas	Arable land	Non-irrigated arable land
			Permanently irrigated land
			Rice fields
		Permanent crops	Vineyards
			Fruit trees and berry plantations
			Olive groves
		Pastures	Pastures
		Heterogeneous agricultural areas	Annual crops associated with permanent crops
			Complex cultivation patterns
			Land principally occupied by agriculture, with significant areas of natural vegetation

			Agro-forestry areas
Forest	Forest and semi natural areas	Forests	Broad-leaved forest
			Coniferous forest
			Mixed forest
Semi-natural	Forest and semi natural areas	Scrub and/or herbaceous vegetation associations	Natural grasslands
			Moors and heathland
			Sclerophyllous vegetation
			Transitional woodland-shrub
		Open spaces with little or no vegetation	Beaches, dunes, sands
			Bare rocks
			Sparsely vegetated areas
			Burnt areas
			Glaciers and perpetual snow
Wetland	Wetlands	Inland wetlands	Inland marshes
			Peat bogs
		Maritime wetlands	Salt marshes
			Salines
			Intertidal flats
	Water bodies	Inland waters	Water courses
			Water bodies

Table A.5.2. Avian functional traits used to explore temporal and spatial trends in functional diversity indices; functional richness, evenness, dispersion, originality and specialisation.

Trait	**Description**	**Rationale**	**Source**	**Type of variable**
Bill length (mm)	From bill tip to skull.	Reflects the shape and size of food items captured and consumed (Díaz *et al*., 2013). Also used as a proxy to describe variation in bird calls and songs (Demery *et al*., 2021).	Tobias *et al*., (2022); Avonet database	Numerical, continuous
Bill width (mm)	Horizontally across widest part of the bill.			
Bill depth (mm)	Vertically down the bill taken in front of the nostrils.			
Tarsus length (mm)	From the base of the toes to tibiotarsal joint.	Reflects micro-habitat utilisation, foraging strategy, dispersal (Stewart *et al*., 2020).		
Kipp's Distance (mm)	Difference in length between wing length (carpal joint to tip of primary feather) and secondary length (carpal joint to tip of first secondary feather).	Reflect movement and dispersal abilities, locomotory behaviour, provide species with ability to withstand environmental changes (Luck *et al*., 2012).		
Wing length (mm)	From carpal joint to wing tip.			
Hand-wing Index (mm)	Kipp's Distance / wing length *100			
Tail length (mm)	From base of tail to tip of longest feathers.			
Weight (g)	A range of techniques including genus averages, morphological models and close relatives as proxies. Mean values were used.	Reflects key aspects of metabolic requirements, movement and foraging behaviour (Stewart *et al*., 2020). Also strongly		

		related to resource use, foraging behaviour, reproductive output, longevity and dispersal abilities (Luck *et al*., 2012).		
Predominant locomotory niche while foraging	Combined trophic and foraging niche classifications from Pigot *et al*., (2020). Species assigned to one of the following four niches; aerial, terrestrial, insessorial and aquatic.	Impact of birds on ecosystem function is primarily related to what they eat and how they obtain food (Luck *et al*., 2013). Related to species' sensitivity to habitat change and resource requirements (Ding *et al*., 2013)		Categorical
Predominant diet	Each species assigned to trophic level from which they obtain at least 60% of their food resources. Species assigned to one of the following ten niches; frugivore, granivore, nectarivore, herbivore, herbivore aquatic, invertivore, vertivore, aquatic predator, scavenger, omnivore (uses multiple niches in equal proportions).			
Migratory status	Each species assigned to one of the following three migratory strategies; sedentary, partially migratory (undergoes short-distance migrations), migratory (long-distance migrations).	Reflects mobility, dispersal capabilities and species ability to adapt to land use change and reduce likelihood of extinction (Sekercioglu, 2012).		
Nest type	Each species assigned to one of the following five nest types; ground, ground close (nest in tussock close to ground), hole (in dead or live tree, bank or ground), open-arboreal (cup in bush, tree, cliff edge), closed-arboreal.	Reflects diversity of habitat use by species. Represents breeding ecology and niche of each species (Pearman *et al*., 2014).	Storchová and Hořák, (2018)	Categorical
Reproductive output	Annual number of clutches x clutch size x egg volume. Egg volume calculated as (0.5 x egg length x egg width)^2	Measure of reproductive success. Reflects reproductive strategy and species ability to recover from disturbance *i.e.*, species with larger clutches and more clutches per year will recolonize more quickly (Newbold *et al*., 2013).	Petchey *et al*., (2007); Storchová and Hořák, (2018)	Numerical, continuous

Extent of habitat association	Species’ European mean RHU score for each of the habitat types in this study were calculated. Mean RHU score used for each species at each site determined by the dominant habitat type at that site.	Influences the spatial distribution and extent of species’ resource use for a given habitat. More specialised species are less able to respond to environmental variation (Sol *et al*., 2002).	Following the methods of O’Reilly *et al.*, (2022), scores were calculated as part of this study	Numerical, continuous
Degree of habitat specialisation	Number of habitats for which each species had a mean European RHU score of ≥1. Degree of habitat specialisation was between one and four.			Categorical
Evolutionary distinctness score	Species-level measure representing the weighted sum of the branch lengths along the path from the root of a tree to a given tip, *i.e.* species.	Reflects species’ contribution to the evolutionary history of the clade and captures uniquely divergent genomes and functions (Jetz *et al*., 2014).	Jetz *et al*., (2014)	Numerical, continuous

Table A.5.3. Functional diversity indices used in this study. In the context of this study, community can be described as the group of species at a given site, in a given year.

Functional diversity index	**Definition**
Functional richness (FRic) (Villéger *et al*., 2008)	Describes the amount of functional trait space occupied by species in a community.
Functional evenness (FEve) (Villéger *et al*., 2008)	Describes the regularity with which species' abundances are distributed in functional trait space (along the shortest minimum spanning tree linking all species).
Functional dispersion (FDis) (Laliberté and Legendre, 2010)	Describes the mean distance of individual species to the centroid of all species in multidimensional trait space, weighted by species' relative abundances.
Functional originality (FOri) (Mouillot *et al*., 2013)	Describes the weighted mean distance of each species to its nearest neighbour in functional trait space. Distances are weighted based on species' relative abundances. Describes the isolation of a species in the functional trait space of a community.
Functional specialisation (FSpe) (Mouillot *et al*., 2013)	Describes the mean distance of a species from the rest of the species pool in functional space.

Table A.5.4. Results of general linear mixed models (GLMMs) for temporal trends in functional diversity indices; functional richness (FRic), functional evenness (FEve), functional dispersion (FDis), functional originality (FOri) and functional specialisation (FSpe) for the full avian community and three subset groups of species; generalists, specialists and visitors for forest and farmland habitat in Europe between 1998 and 2017. Annual values for each index were standardised at the site-level prior to analyses. Significant values are highlighted in bold.

			FRic					FEve					FDis					FOri					FSpe				
		Fixed effects	Estimate (SE)	t	Chi	df	p	Estimate (SE)	t	Chi	df	p	Estimate (SE)	t	Chi	df	p	Estimate (SE)	t	Chi	df	p	Estimate (SE)	t	Chi	df	p
Forest	All species	Longitude	7.09e-05 (0.000757)	0.094	0.0087695	1	0.925	9.82e-05 (0.000757)	0.13	0.0168354	1	0.897	-7.81e-05 (0.0007568)	-0.103	0.0106484	1	0.918	-0.0001719 (0.0007566)	-0.227	0.0516445	1	0.82	0.0002391 (0.000756)	0.316	0.1000054	1	0.752
		Latitude	-0.000135 (0.00104)	-0.13	0.0169477	1	0.896	8.82e-05 (0.00104)	0.085	0.0072615	1	0.932	-0.0002924 (0.0010347)	-0.283	0.0798654	1	0.777	0.000232 (0.0010344)	0.224	0.0502794	1	0.823	-0.0006099 (0.0010336)	-0.59	0.348128	1	0.555
		Year	0.000194 (0.0026)	0.075	0.0055742	1	0.94	-0.00497 (0.0024)	-2.074	4.3013207	1	**0.038**	0.0053149 (0.00265)	2.006	4.0225236	1	**0.045**	0.0019433 (0.0028961)	0.671	0.4502361	1	0.502	0.0001525 (0.003317)	0.046	0.0021151	1	0.963
	Generalists	Longitude	9.3e-05 (0.000985)	0.094	0.0089265	1	0.925	8.6e-05 (0.000985)	0.087	0.0076226	1	0.93	-9.02e-05 (0.0009846)	-0.092	0.0083913	1	0.927	0.0001173 (0.0009829)	0.119	0.01425	1	0.905	0.0002688 (0.0009782)	0.275	0.0755234	1	0.783
		Latitude	-0.000249 (0.00122)	-0.204	0.0417949	1	0.838	7.32e-05 (0.00122)	0.06	0.0036135	1	0.952	-0.0001165 (0.0012183)	-0.096	0.0091491	1	0.924	0.000272 (0.0012164)	0.224	0.0499993	1	0.823	-0.0003003 (0.0012107)	-0.248	0.0615245	1	0.804
		Year	0.00218 (0.00231)	0.943	0.8886655	1	0.346	-0.0056 (0.00251)	-2.229	4.9680102	1	**0.026**	0.002321 (0.0025588)	0.907	0.8227527	1	0.364	-0.0103741 (0.0034659)	-2.993	8.9593093	1	**0.003**	0.0007214 (0.005077)	0.142	0.0201914	1	0.887
	Specialists	Longitude	-0.0001973 (0.0009527)	-0.207	0.0428722	1	0.836	-0.000153 (0.000955)	-0.16	0.0255179	1	0.873	0.0003775 (0.0009483)	0.398	0.1584582	1	0.691	-2.33e-05 (0.000953)	-0.024	0.0005997	1	0.98	0.0004321 (0.0009452)	0.457	0.2089403	1	0.648
		Latitude	-0.000105 (0.0013092)	-0.08	0.0064324	1	0.936	3.09e-05 (0.00131)	0.024	0.0005538	1	0.981	-0.0010083 (0.0013031)	-0.774	0.5986792	1	0.439	-0.000476 (0.00131)	-0.363	0.1321154	1	0.716	-0.0013028 (0.001299)	-1.003	1.005787	1	0.316
		Year	0.00644 (0.0032741)	1.967	3.8689434	1	**0.049**	0.00523 (0.00239)	2.188	4.7893085	1	**0.029**	-0.0038363 (0.0050663)	-0.757	0.5733612	1	0.449	0.00443 (0.00342)	1.296	1.678645	1	0.195	-0.0094911 (0.0058449)	-1.624	2.6368714	1	0.104
	Visitors	Longitude	-3.8e-06 (0.000852)	-0.004	1.99E-05	1	0.996	0.0002445 (0.0008508)	0.287	0.0825777	1	0.774	2.84e-06 (0.000849)	0.003	1.12E-05	1	0.997	-4.67e-05 (0.000852)	-0.055	0.0030014	1	0.956	-0.0005377 (0.0008478)	-0.634	0.4022291	1	0.526
		Latitude	-0.000133 (0.00126)	-0.105	0.011072	1	0.916	-0.0001489 (0.001262)	-0.118	0.0139249	1	0.906	-0.000548 (0.00126)	-0.435	0.1889963	1	0.664	-0.000293 (0.00126)	-0.231	0.0535415	1	0.817	-0.0002021 (0.0012578)	-0.161	0.0258126	1	0.872
		Year	-0.00126 (0.00272)	-0.464	0.2149597	1	0.643	-0.0059256 (0.0013332)	-4.445	19.753716	1	**<0.001**	-0.000721 (0.00413)	-0.175	0.0305234	1	0.861	0.00101 (0.00252)	0.403	0.162495	1	0.687	0.0130157 (0.0045635)	2.852	8.1346819	1	**0.004**
Farmland	All species	Longitude	-0.0004823 (0.0004221)	-1.143	1.3060986	1	0.253	1.04e-05 (0.000422)	0.025	0.000606	1	0.98	-0.0008597 (0.0004202)	-2.046	4.1860735	1	**0.041**	0.0007027 (0.000422)	1.665	2.7725159	1	0.096	-0.0011497 (0.0004196)	-2.74	7.5052536	1	**0.006**
		Latitude	0.000447 (0.0009487)	0.471	0.2219883	1	0.638	-8.76e-05 (0.00095)	-0.092	0.0085053	1	0.927	0.0004066 (0.0009469)	0.429	0.1843931	1	0.668	-0.0007307 (0.0009486)	-0.77	0.5933651	1	0.441	0.0005475 (0.0009452)	0.579	0.3355809	1	0.562
		Year	0.0067729 (0.0025652)	2.64	6.9710808	1	**0.008**	-0.00109 (0.00129)	-0.845	0.7138138	1	0.398	0.0130848 (0.0009785)	13.372	178.8194806	1	**<0.001**	-0.009618 (0.0026204)	-3.67	13.472232	1	**<0.001**	0.0168703 (0.0011601)	14.542	211.4616947	1	**<0.001**
	Generalists	Longitude	-6.46e-06 (0.000438)	-0.015	0.0002177	1	0.988	0.0001392 (0.000437)	0.318	0.1014154	1	0.75	-0.000233 (0.000437)	-0.533	0.2836871	1	0.594	-0.0008543 (0.0004376)	-1.952	3.8108412	1	0.051	-0.0012936 (0.0004361)	-2.966	8.7977543	1	**0.003**

	Latitude	0.000357 (0.000986)	0.362	0.1307667	1	0.718	-4.62e-05 (0.0009865)	-0.047	0.0021932	1	0.963	-4.06e-05 (0.000983)	-0.041	0.0017073	1	0.967	0.0009173 (0.000985)	0.931	0.8671989	1	0.352	0.0007308 (0.0009813)	0.745	0.5545894	1	0.456
	Year	0.000125 (0.00256)	0.049	0.0023784	1	0.961	-0.0024328 (0.0009401)	-2.588	6.6968907	1	**0.01**	0.00505 (0.00401)	1.258	1.5814352	1	0.209	0.0104185 (0.0032048)	3.251	10.5685126	1	**0.001**	0.0183677 (0.0044961)	4.085	16.6895717	1	**<0.001**
Specialists	**Longitude**	-0.0001704 (0.0005445)	-0.313	0.0979163	1	0.754	-0.000315 (0.000544)	-0.578	0.3340459	1	0.563	-0.0010713 (0.0005441)	-1.969	3.8763125	1	**0.049**	0.0010533 (0.0005441)	1.936	3.7478207	1	0.053	-0.0005661 (0.000543)	-1.043	1.0868441	1	0.297
	Latitude	-0.0001348 (0.0012457)	-0.108	0.0117144	1	0.914	8.84e-05 (0.00125)	0.071	0.0050277	1	0.943	0.0009728 (0.0012446)	0.782	0.6108853	1	0.434	-0.000908 (0.0012434)	-0.73	0.5333362	1	0.465	0.0004403 (0.0012454)	0.354	0.1249911	1	0.724
	Year	0.0043868 (0.0023679)	1.853	3.4322324	1	0.064	0.00549 (0.00136)	4.037	16.2984912	1	**<0.001**	0.013757 (0.0024583)	5.596	31.3160474	1	**<0.001**	-0.0100617 (0.0038077)	-2.642	6.9824771	1	**0.008**	0.0082785 (0.0010515)	7.873	61.9794469	1	**<0.001**
Visitors	**Longitude**	3.82e-05 (0.000488)	0.078	0.0061269	1	0.938	0.0003335 (0.0004862)	0.686	0.4705887	1	0.493	-0.0002112 (0.0004884)	-0.432	0.1870177	1	0.665	0.000324 (0.000488)	0.664	0.4403727	1	0.507	-0.0007443 (0.0004872)	-1.528	2.3333351	1	0.127
	Latitude	-0.00021 (0.00111)	-0.189	0.0357533	1	0.85	-0.0002984 (0.0011075)	-0.269	0.0725863	1	0.788	0.0001008 (0.0011096)	0.091	0.0082484	1	0.928	-9.04e-06 (0.00111)	-0.008	6.67E-05	1	0.993	0.0001819 (0.0011052)	0.165	0.0270925	1	0.869
	Year	0.00238 (0.00174)	1.369	1.873186	1	0.171	-0.0056083 (0.0008141)	-6.889	47.4561595	1	**<0.001**	0.0045046 (0.0018235)	2.47	6.1026709	1	**0.013**	-0.00922 (0.00341)	-2.708	7.3314244	1	**0.007**	0.0108196 (0.0039291)	2.754	7.5829905	1	**0.006**

Table A.5.5. Results for GLMMs that compare temporal trends across species groups; full avian community, generalists, specialists and visitors for each functional diversity index; functional richness (FRic), functional evenness (FEve), functional dispersion (FDis), functional originality (FOri) and functional specialisation (FSpe) in forest and farmland habitats. Annual values for each index were standardised at the site-level prior to analyses.

		FRic			**FEve**			**FDis**			**FOri**			**FSpe**		
	Fixed effects	**Estimate**	**Std. Error**	**t**	**Estimate**	**Std. Error**	**t**	**Estimate**	**Std. Error**	**t**	**Estimate**	**Std. Error**	**t**	**Estimate**	**Std. Error**	**t**
Forest	**Year**	-0.000164	0.00238	-0.069	-0.0047	0.0016	-2.943	0.0044	0.0025	1.758	0.000821	0.00166	0.493	-0.00035	0.00407	-0.086
	Latitude	-0.000183	0.000595	-0.308	-1.49E-05	0.000595	-0.025	-0.000457	0.000595	-0.769	-1.82E-05	0.000595	-0.031	-0.000619	0.000594	-1.043
	Longitude	1.02E-05	0.000436	0.023	9.12E-05	0.000436	0.209	3.08E-05	0.000436	0.071	-5.47E-05	0.000436	-0.125	0.000137	0.000435	0.314
	Generalists	-0.026	0.0225	-1.153	0.0116	0.0226	0.514	0.0364	0.0225	1.615	0.126	0.0226	5.583	-0.000381	0.0225	-0.017
	Specialists	-0.085	0.022	-3.865	-0.112	0.022	-5.069	0.0904	0.022	4.107	-0.0497	0.022	-2.256	0.0858	0.022	3.907
	Visitors	0.00915	0.0217	0.422	0.0162	0.0217	0.747	0.0522	0.0217	2.404	-0.00603	0.0217	-0.278	-0.148	0.0217	-6.844
	Year:Generalists	0.00212	0.00171	1.24	-0.000906	0.00171	-0.531	-0.003	0.00171	-1.761	-0.0103	0.00171	-6.02	7.28E-05	0.0017	0.043

	Year:Specialists	0.00692	0.00167	4.15	0.00917	0.00167	5.491	-0.00744	0.00167	-4.461	0.00406	0.00167	2.43	-0.00701	0.00166	-4.214
	Year:Visitors	-0.000789	0.00166	-0.475	-0.00139	0.00166	-0.836	-0.0043	0.00166	-2.586	0.000521	0.00166	0.313	0.0124	0.00166	7.482
Farmland	**Year**	0.0066344	0.0019634	3.379	-0.000948	0.000943	-1.005	0.0129375	0.002283	5.667	-0.0087687	0.0018844	-4.653	0.016821	0.0010334	16.277
	Latitude	0.0001667	0.0005272	0.316	-0.000143	0.000527	-0.27	0.0003065	0.000527	0.582	-0.0001082	0.0005268	-0.205	0.0005436	0.0005257	1.034
	Longitude	-0.0001766	0.0002333	-0.757	7.18E-05	0.000233	0.308	-0.0005986	0.0002333	-2.566	0.0002248	0.0002331	0.964	-0.0010018	0.0002323	-4.313
	Generalists	0.0854406	0.0122722	6.962	0.0211	0.0123	1.717	0.0906643	0.0122669	7.391	-0.2200416	0.012264	-17.942	-0.0178619	0.0122434	-1.459
	Specialists	0.0190108	0.0141648	1.342	-0.076	0.0142	-5.356	-0.0018632	0.0141587	-0.132	0.0185595	0.0141554	1.311	0.1098803	0.0141316	7.776
	Visitors	0.0438728	0.0127702	3.436	0.0587	0.0128	4.589	0.1006928	0.0127647	7.888	0.0065256	0.0127618	0.511	0.0599252	0.0127403	4.704
	Year:Generalists	-0.0071863	0.0009431	-7.62	-0.00177	0.000944	-1.87	-0.0076345	0.0009426	-8.099	0.0184638	0.0009424	19.592	0.0014574	0.0009408	1.549
	Year:Specialists	-0.0016376	0.0010877	-1.506	0.00637	0.00109	5.846	0.0001472	0.0010872	0.135	-0.0015114	0.001087	-1.39	-0.0091886	0.0010852	-8.468
	Year:Visitors	-0.0037198	0.0009804	-3.794	-0.0049	0.000982	-4.994	-0.008497	0.00098	-8.671	-0.0004974	0.0009797	-0.508	-0.0051126	0.0009781	-5.227

Table A.5.6. Chi^2, degrees of freedom (df) and p-values (p) for GLMMs that compare temporal trends across species groups; full avian community, generalists, specialists and visitors for each functional diversity index; functional richness (FRic), functional evenness (FEve), functional dispersion (FDis), functional originality (FOri) and functional specialisation (FSpe) in forest and farmland habitats. Annual values for each index were standardised at the site-level prior to analyses. Significant values highlighted in bold.

		FRic			**FEve**			**FDis**			**FOri**			**FSpe**		
		Chi	**df**	**p**	**Chi**	**df**	**p**	**Chi**	**df**	**p**	**Chi**	**df**	**p**	**Chi**	**df**	**p**
Forest	**Year**	0.6144725	1	0.433	5.5296044	1	0.019	0.1769648	1	0.674	0.0579864	1	0.81	0.0635739	1	0.801
	Latitude	0.0949572	1	0.758	0.0006301	1	0.98	0.591238	1	0.442	0.0009369	1	0.976	1.0888333	1	0.297
	Longitude	0.0005483	1	0.981	0.0436646	1	0.834	0.0049958	1	0.944	0.0157181	1	0.9	0.098465	1	0.754
	group	0.0043667	3	1	0.0059945	3	1	0.0034431	3	1	0.0004451	3	1	0.0106809	3	1
	Year:group	23.6391367	3	**<0.001**	47.7329524	3	**<0.001**	20.5532275	3	**<0.001**	68.7878794	3	**<0.001**	125.7243975	3	**<0.001**
Farmland	**Year**	3.2633259	1	0.071	4.1122079	1	0.043	15.4860449	1	<0.001	4.745155	1	0.029	270.5665731	1	<0.001
	Latitude	0.1000074	1	0.752	0.0730051	1	0.787	0.338219	1	0.561	0.0422022	1	0.837	1.069525	1	0.301

Longitude	0.5730345	1	0.449	0.0950323	1	0.758	6.5867946	1	0.01	0.9300354	1	0.335	18.5999953	1	<0.001
group	0.010066	3	1	0.0004103	3	1	0.0227028	3	0.999	0.0068657	3	1	0.0663457	3	0.996
Year:group	62.2377427	3	**<0.001**	103.3649327	3	**<0.001**	126.8736166	3	**<0.001**	569.6629965	3	**<0.001**	121.900682	3	**<0.001**

Table A.5.7. Results for pairwise comparison of temporal trends between each pair of species groups for each functional diversity index; functional richness (FRic), functional evenness (FEve), functional dispersion (FDis), functional originality (FOri) and functional specialisation (FSpe). Annual values for each index were standardised at the site-level prior to analyses. Significant values highlighted in bold.

		FRic			**FEve**			**FDis**			**FOri**			**FSpe**		
Habitat	**Pairwise comparison**	**Estimate (SE)**	**z**	**p**	**Estimate (SE)**	**z**	**p**	**Estimate (SE)**	**z**	**p**	**Estimate (SE)**	**z**	**p**	**Estimate (SE)**	**z**	**p**
Forest	**All species - Generalists**	-0.0021 (0.002)	-1.24	0.766	9e-04 (0.002)	0.531	0.996	0.003 (0.002)	1.761	0.386	0.0103 (0.002)	6.02	**<0.001**	-1e-04 (0.002)	-0.043	1
	All species - Specialists	-0.0069 (0.002)	-4.15	**<0.001**	-0.0092 (0.002)	-5.491	**<0.001**	0.0074 (0.002)	4.461	**<0.001**	-0.0041 (0.002)	-2.43	0.087	0.007 (0.002)	4.214	**<0.001**
	All species - Visitors	8e-04 (0.002)	0.475	0.998	0.0014 (0.002)	0.836	0.955	0.0043 (0.002)	2.586	0.057	-5e-04 (0.002)	-0.313	1	-0.0124 (0.002)	-7.482	**<0.001**
	Generalists - Specialists	-0.0048 (0.002)	-2.651	**0.047**	-0.0101 (0.002)	-5.552	**<0.001**	0.0044 (0.002)	2.446	0.083	-0.0143 (0.002)	-7.904	**<0.001**	0.0071 (0.002)	3.918	**0.001**
	Generalists - Visitors	0.0029 (0.002)	1.607	0.497	5e-04 (0.002)	0.268	1	0.0013 (0.002)	0.716	0.979	-0.0108 (0.002)	-5.97	**<0.001**	-0.0123 (0.002)	-6.839	**<0.001**
	Specialists - Visitors	0.0077 (0.002)	4.352	**<0.001**	0.0106 (0.002)	5.954	**<0.001**	-0.0031 (0.002)	-1.772	0.379	0.0035 (0.002)	1.994	0.247	-0.0194 (0.002)	-10.988	**<0.001**
Farmland	**All species - Generalists**	0.0072 (0.001)	7.62	**<0.001**	0.0018 (0.001)	1.87	0.317	0.0076 (0.001)	8.099	**<0.001**	-0.0185 (0.001)	-19.592	**<0.001**	-0.0015 (0.001)	-1.549	0.54
	All species - Specialists	0.0016 (0.001)	1.506	0.573	-0.0064 (0.001)	-5.846	**<0.001**	-1e-04 (0.001)	-0.135	1	0.0015 (0.001)	1.39	0.66	0.0092 (0.001)	8.468	**<0.001**
	All species - Visitors	0.0037 (0.001)	3.794	**0.001**	0.0049 (0.001)	4.994	**<0.001**	0.0085 (0.001)	8.671	**<0.001**	5e-04 (0.001)	0.508	0.997	0.0051 (0.001)	5.227	**<0.001**
	Generalists - Specialists	-0.0055 (0.001)	-5.053	**<0.001**	-0.0081 (0.001)	-7.397	**<0.001**	-0.0078 (0.001)	-7.09	**<0.001**	0.02 (0.001)	18.204	**<0.001**	0.0106 (0.001)	9.718	**<0.001**
	Generalists - Visitors	-0.0035 (0.001)	-3.495	**0.003**	0.0031 (0.001)	3.159	**0.009**	9e-04 (0.001)	0.87	0.946	0.019 (0.001)	19.13	**<0.001**	0.0066 (0.001)	6.64	**<0.001**
	Specialists - Visitors	0.0021 (0.001)	1.842	0.334	0.0113 (0.001)	9.958	**<0.001**	0.0086 (0.001)	7.651	**<0.001**	-0.001 (0.001)	-0.898	0.937	-0.0041 (0.001)	-3.615	**0.002**

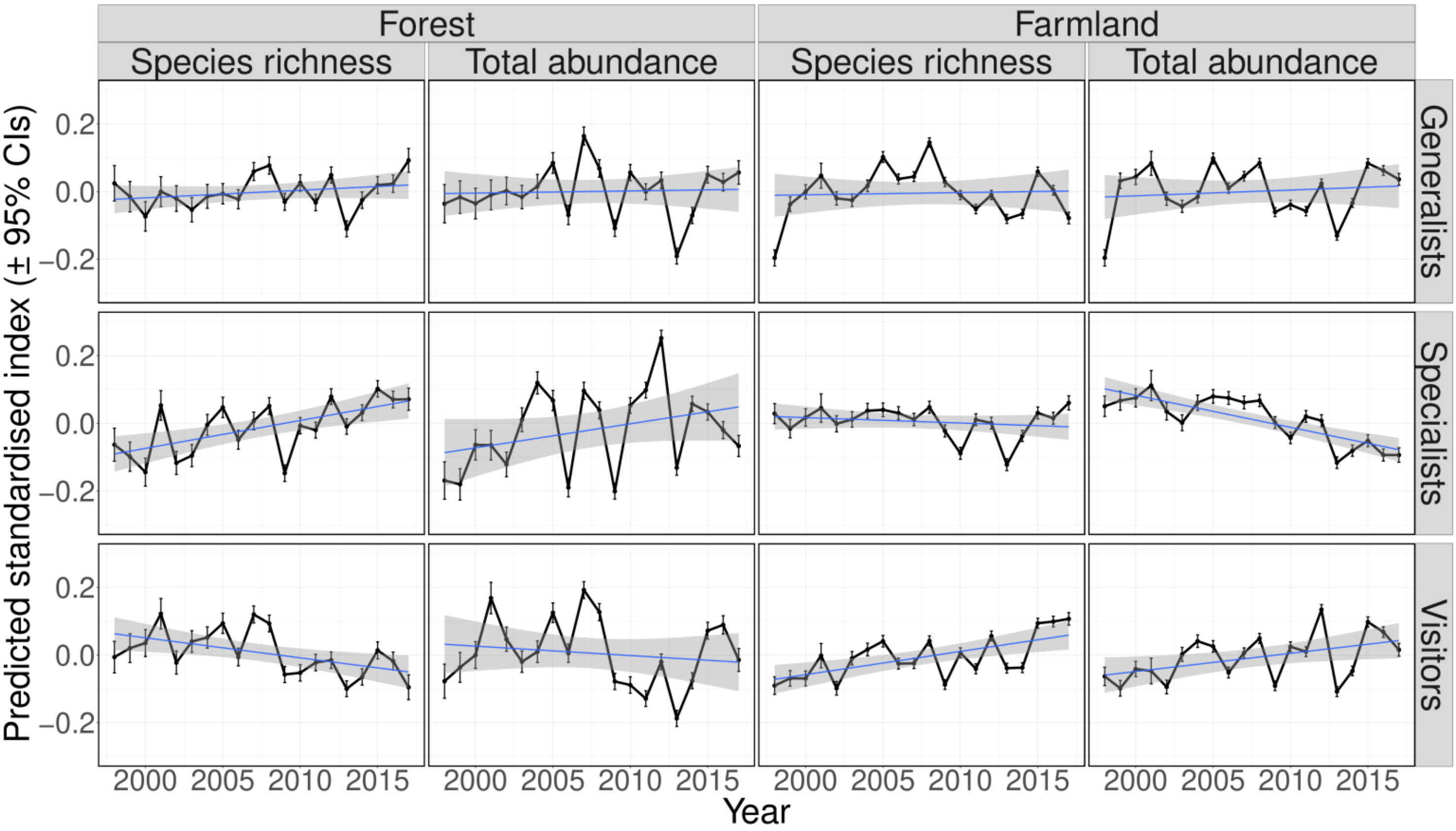


Fig. A.5.1. Temporal trends in species richness and total abundance in Europe between 1998 to 2017 for generalists, specialists and visitors. Annual values were standardised at the site-level prior to analyses. Solid straight line in each case represents the predicted trend from GLMMs (with year as continuous variable) with shaded areas indicating 95% confidence intervals. Points in each panel represent the mean annual values with vertical lines either side of the points representing standard error for that index and species group in that year.

Table A.5.8. Results of general linear mixed models (GLMMs) for temporal trends in species richness and total abundance for generalists, specialists and visitors for forest and farmland habitat in Europe between 1998 and 2017. Annual values for each index were standardised at the site-level prior to analyses. Significant values are highlighted in bold.

			Species richness					**Total abundance**				
		Fixed effects	**Estimate (SE)**	**t**	**Chi2**	**df**	**p**	**Estimate (SE)**	**t**	**Chi2**	**df**	**p**
Forest	**Generalists**	**Latitude**	-0.0002355 (0.0012132)	-0.194	0.0376852	1	0.846	-0.0001503 (0.0012164)	-0.124	0.0152631	1	0.902
		Longitude	6.19e-05 (0.0009805)	0.063	0.0039853	1	0.95	0.0002112 (0.0009829)	0.215	0.0461644	1	0.83
		Year	0.0021846 (0.0023735)	0.92	0.8471942	1	0.357	0.0004309 (0.0034778)	0.124	0.0153517	1	0.901
	Specialists	**Latitude**	5.65e-05 (0.00131)	0.043	0.0018749	1	0.965	0.0005451 (0.0013038)	0.418	0.1747914	1	0.676
		Longitude	-0.000327 (0.00095)	-0.344	0.118325	1	0.731	-0.0002964 (0.0009487)	-0.312	0.0975782	1	0.755
		Year	0.00834 (0.00311)	2.683	7.1999346	1	**0.007**	0.0069733 (0.0049123)	1.42	2.0151859	1	0.156
	Visitors	**Latitude**	1.7e-05 (0.00126)	0.013	0.0001815	1	0.989	-2.53e-05 (0.00126)	-0.02	0.0004027	1	0.984
		Longitude	0.000189 (0.00085)	0.222	0.0493161	1	0.824	7.69e-05 (0.000849)	0.091	0.0082124	1	0.928
		Year	-0.0061 (0.00283)	-2.159	4.6612562	1	**0.031**	-0.00292 (0.00419)	-0.697	0.4861012	1	0.486
Farmland	**Generalists**	**Latitude**	0.0007404 (0.0009853)	0.751	0.564651	1	0.452	0.0001305 (0.0009859)	0.132	0.0175146	1	0.895
		Longitude	-0.000175 (0.0004376)	-0.4	0.1598241	1	0.689	-0.0001261 (0.0004379)	-0.288	0.0829703	1	0.773
		Year	0.0006546 (0.0027296)	0.24	0.0575147	1	0.81	0.0017806 (0.0027953)	0.637	0.4057644	1	0.524
	Specialists	**Latitude**	-0.0002228 (0.0012368)	-0.18	0.0324477	1	0.857	-0.0001682 (0.0012462)	-0.135	0.0182079	1	0.893
		Longitude	0.0001884 (0.0005404)	0.349	0.12149	1	0.727	0.0005406 (0.0005446)	0.993	0.9853333	1	0.321
		Year	-0.0015788 (0.0020336)	-0.776	0.602743	1	0.438	-0.0095768 (0.0021772)	-4.399	19.3490925	1	**<0.001**
	Visitors	**Latitude**	0.0001853 (0.0011079)	0.167	0.0279571	1	0.867	0.0003225 (0.0011082)	0.291	0.0846794	1	0.771
		Longitude	-0.0003025 (0.0004881)	-0.62	0.3841491	1	0.535	-0.000309 (0.0004883)	-0.633	0.4004406	1	0.527
		Year	0.0069686 (0.0025217)	2.763	7.6367177	1	**0.006**	0.0053796 (0.0027869)	1.93	3.7260767	1	0.054

Table A.5.9. Results of general linear mixed models (GLMMs) for standardised effect size in functional richness (FRic) for three subset groups of species; generalists, specialists and visitors for forest and farmland habitat in Europe between 1998 and 2017. Significant values are highlighted in bold.

		Fixed effects	**Estimate**	**Std.Error**	**t**	**Chi2**	**df**	**p**
Forest	**Generalists**	**Latitude**	0.0132019	0.0031396	4.205	17.6816121	1	**<0.001**
		Longitude	-0.0132156	0.0025596	-5.163	26.6574372	1	**<0.001**
		Year	0.0003818	0.0008795	0.434	0.1884662	1	0.664
	Specialists	**Latitude**	0.0299792	0.0032245	9.297	86.4423491	1	**<0.001**
		Longitude	0.0036245	0.0023767	1.525	2.3256984	1	0.127
		Year	-0.0030973	0.0004492	-6.895	47.5343241	1	**<0.001**
	Visitors	**Latitude**	0.057777	0.005327	10.845	117.6180034	1	**<0.001**
		Longitude	0.007672	0.00392	1.957	3.8305392	1	**0.05**
		Year	0.001211	0.001982	0.611	0.3732123	1	0.541
Farmland	**Generalists**	**Latitude**	0.0390571	0.0030445	12.829	164.571613	1	**<0.001**
		Longitude	-0.0096756	0.002287	-4.231	17.899497	1	**<0.001**
		Year	0.0027369	0.0006437	4.252	18.0804935	1	**<0.001**
	Specialists	**Latitude**	-0.0177744	0.0022763	-7.809	60.9739766	1	**<0.001**
		Longitude	-0.0208599	0.0017577	-11.867	140.8373958	1	**<0.001**
		Year	0.0004264	0.0009309	0.458	0.2098058	1	0.647
	Visitors	**Latitude**	0.039041	0.003608	10.821	117.0919725	1	**<0.001**
		Longitude	-0.01284	0.002707	-4.743	22.4969089	1	**<0.001**
		Year	-0.003696	0.000964	-3.834	14.6981543	1	**<0.001**

Table A.5.10. Results of GLMMs that explore spatial variation in the standardised effect size of functional richness (FRic) for generalists, specialists and visitors in forest and farmland habitat in Europe between 1998 and 2017. Significant values highlighted in bold.

		Fixed effects	**Estimate (Std.Error)**	**t**	**Chi2**	**df**	**p**
Forest	**Generalists**	**Latitude**	0.0127 (0.00346)	3.657	17.5720801	1	<0.001
		Longitude	-0.0151 (0.00283)	-5.332	26.6652333	1	<0.001
		Year	-0.00344 (0.00573)	-0.6	0.194543	1	0.659
		Year:Latitude	3.93e-05 (0.000115)	0.343	0.1175946	1	0.732
		Year:Longitude	0.000145 (9.34e-05)	1.554	2.4143297	1	0.12
	Specialists	**Latitude**	0.034 (0.00344)	9.884	85.9929773	1	<0.001
		Longitude	0.00369 (0.00254)	1.455	2.1722572	1	0.141
		Year	0.0135 (0.00448)	3.018	45.1671222	1	<0.001
		Year:Latitude	-0.00031 (9.05e-05)	-3.422	11.7079071	1	**0.001**
		Year:Longitude	-1.42e-05 (6.66e-05)	-0.213	0.0452494	1	0.832
	Visitors	**Latitude**	0.055 (0.0055)	9.996	117.2649403	1	<0.001
		Longitude	0.0113 (0.00403)	2.808	3.8464764	1	0.05
		Year	-0.00811 (0.00594)	-1.366	0.3606358	1	0.548
		Year:Latitude	0.000222 (0.000111)	1.998	3.9938628	1	**0.046**
		Year:Longitude	-0.000284 (7.26e-05)	-3.907	15.2636668	1	**<0.001**
Farmland	**Generalists**	**Latitude**	0.0368 (0.00325)	11.319	164.7165544	1	<0.001
		Longitude	-0.00955 (0.00234)	-4.08	17.4720458	1	<0.001
		Year	-0.00682 (0.00488)	-1.398	18.065432	1	<0.001
		Year:Latitude	0.000185 (9.33e-05)	1.978	3.9137658	1	**0.048**

	Year:Longitude	-1.24e-06 (3.94e-05)	-0.032	0.0009929	1	0.975
Specialists	**Latitude**	-0.0148 (0.00252)	-5.88	61.0428523	1	<0.001
	Longitude	-0.0206 (0.00183)	-11.296	143.0756864	1	<0.001
	Year	0.0133 (0.00476)	2.785	0.2137214	1	0.644
	Year:Latitude	-0.000246 (9.02e-05)	-2.724	7.4205351	1	**0.006**
	Year:Longitude	-3.44e-05 (3.85e-05)	-0.894	0.7993913	1	0.371
Visitors	**Latitude**	0.043 (0.00386)	11.156	116.9470567	1	<0.001
	Longitude	-0.0148 (0.00277)	-5.34	23.0962603	1	<0.001
	Year	0.0127 (0.00572)	2.212	16.3890444	1	<0.001
	Year:Latitude	-0.00032 (0.000109)	-2.941	8.6478461	1	**0.003**
	Year:Longitude	0.000141 (4.56e-05)	3.094	9.5735376	1	**0.002**

Chapter Six: General conclusions

6.1 Harnessing quantitative methods to improve and extend biodiversity indicators

Despite global efforts and international cooperation to tackle the biodiversity crisis (Walpole *et al*., 2009; Heink & Kowarik, 2010; Mace *et al*., 2018) (Secretariat of the Convention on Biological Diversity, 2000, 2002), global biodiversity continues to decline due to ongoing land use change, habitat degradation and overexploitation of species (Butchart *et al*., 2010; Mace *et al*., 2018; Díaz *et al*., 2019; Buchanan *et al*., 2020; Pascual *et al*., 2021) (IPBES, 2019; WWF, 2022). Biodiversity indicators have played a vital role in tracking these population declines (CBD, 2010; Walpole *et al.*, 2009) and indices of ecosystem function have monitored changes in overall community functional structure to determine ecosystem service sustainability in the face of these environmental stressors (Tilman, 1997; Díaz *et al*., 2006; Cadotte *et al*., 2011; Díaz *et al*., 2013; Mouillot *et al*., 2013). However, studies have suggested that to improve the use of biodiversity indicators, a more objective and systematic approach to indicator species selection is needed in order to standardise the selection process (Hilty & Merenlender, 2000; Fraixedas *et al*., 2020). In addition, functional diversity research in conservation science has grown in popularity over the past two decades (Mammola *et al*., 2021), with several studies exploring temporal and spatial patterns in local-scale functional diversity. However, there is more to learn of temporal and spatial patterns in functional diversity at the larger spatial scale.

The research in this thesis therefore used birds as a model system to improve and extend the use of biodiversity indicators by developing a quantitative and objective approach to indicator species selection and exploring trends from the resultant indicators. Site-level count data and functional trait data for birds were also used in this thesis to improve our understanding of temporal and spatial differences in functional diversity of avian communities at the European level. In addition, research in this thesis harnessed bird data to extend the use of functional diversity indices by exploring temporal and spatial patterns in species subsets within avian communities in order to describe overall patterns.

6.2 Literature-based classifications reflect quantitative metrics for species' habitat association and degree of specialisation

In order for biodiversity indicators to be policy-relevant, they must be representative of wider biodiversity across spatial and temporal scales and responsive to environmental changes (Carignan & Villard, 2002; Gregory *et al*., 2005; Gregory & Strien, 2010). To meet these requirements, a formal and objective process to indicator species selection is needed (Hilty & Merenlender, 2000) and studies have suggested that quantitative methods offer an unbiased and reliable approach to this (Fraixedas *et al.*, 2020). (Butler *et al*., 2012) suggested such a method, *i.e.,* niche-based framework, however aspects of this framework still rely on expert opinion which introduces an element of bias and potential subjectivity. Replacing expert opinion with objective criteria within this framework would remove this subjectivity from the species selection process. In **Chapter two**, I found that literature-based classifications (which are similar to expert opinions as experts often base their opinion on previous research) reflect RHU when defining species' habitat associations and degree of specialisation. This suggests that although the current, expert-based approach to indicator species selection is reliable, quantitative-based assessments, such as RHU are more informative and robust as they can be updated regularly and account for spatial and temporal differences in the extent of species' habitat associations.

6.3 "Direct" indicators are more responsive to environmental changes and representative of wider biodiversity than "top-down" or "bottom-up" indicators

Integrating RHU and the niche-based framework, I found in **Chapter three** that MSI trends for “direct”, “top-down” and “bottom-up” niche-based indicators at the European, regional and national levels generally reflected one another. However, “direct” indicators *i.e.,* those produced at a given spatial scale, covered more resources at that scale and contained species that were more sensitive to changes in resource availability than “top-down” or “bottom-up” indicators. This suggests that despite no significant differences between MSI trends for a given spatial scale within the timeframe of this research, in the future “direct” indicators will be more sensitive to potential changes in resource availability. Although species composition of “direct” indicator sets across regions and countries varied, each set represents the same resource requirements matrix. Therefore the same stressors on forest ecosystems are represented across the indicators due to the underlying concept of the niche-based framework and objective nature of the species selection process. This allows indicators to be comparable over space and time. If adopted, niche-based “direct” indicators would ensure that land-management and policy decisions are targeted appropriately at all spatial and temporal scales.

6.4 Temporal and spatial patterns in functional diversity vary between habitats and indices

Increasingly studies are highlighting the relationship between biodiversity and ecosystem functioning, with higher levels of biodiversity associated with increased ecosystem service provision (Tilman, 1997; Hooper, 1998; Loreau, 1998; Petchey *et al*., 2004). Therefore, studying more nuanced aspects of biodiversity, such as functional diversity, allows us to move beyond simple measures of species richness and increase our understanding of community assembly processes (Mouillot *et al*., 2007; Cadotte *et al*., 2011; Mason *et al*., 2012; Díaz *et al*., 2013). In **Chapter four** I found that temporal and spatial patterns in FD indices varied, with the extent of this variation differing between habitats and indices. Despite most natural habitats experiencing significant land-use change and modification due to anthropogenic activities, this research finds that these activities do not affect all habitats equally *i.e.*, land-use change does not cause universal declines in FD. This is an important and interesting result as this suggests that despite changes in species richness and abundance found in this research, functional diversity and therefore ecosystem service provision may not be effected by land-use change. However, changes in community structure and species' abundances over space and time suggest that species fulfilling those functional roles within a community may be changing.

6.5 Functional diversity patterns of community subsets can explain drivers of overall community change

In **Chapter five** I expanded on this question and explored temporal changes in functional diversity for species subsets (generalists, specialists and visitors) in forest and farmland to understand the potential mechanisms that may drive changes in the overall avian community. I found that the rate of change in functional diversity indices at the subset level reflected trends seen for the full community, however the extent of this relationship varied between subsets, indices and habitats. My expectations prior to analysis were that given significant land-use changes driven by harmful anthropogenic activity (Julliard *et al*., 2006; Smart *et al*., 2006; Devictor *et al*., 2008; Clavel *et al*., 2011), there would be overall declines in functional diversity of avian communities. However, I find that functional diversity overall remains stable or even increases while species' abundances become more unevenly distributed over time for the full avian community and species subsets. This suggests that during the timeframe of this study, ecosystem functionality is protected against changing environmental conditions by changes in the relative abundance of functionally similar species (Naeem & Li, 1997). However, future environmental changes which negatively affect highly abundant species that fulfil important ecosystem functions may have a significant impact on overall ecosystem stability (Wittebolle *et al.,* 2009).

6.6 Using the updated European Forest Bird Indicator from this study to inform conservation policy

Research from this thesis which explored methods for improving and extending the use of biodiversity indicators aims to directly inform conservation policy at the European level. Prior to beginning this PhD, PECBMS and Forest Europe agreed that the current European Forest Bird Indicator should be revised and potentially updated in order to remove the potential bias associated with expert opinion and to ensure that the indicator included species that were sensitive to environmental changes. A quantitative, niche-based framework approach was suggested as the most reliable option for further consideration (Forest Europe, 2019). The integrated RHU and niche-based framework approach developed in this study provides a flexible and robust approach to indicator species selection that can be updated regularly over space and time, if the underlying data are available. In the coming months, results from **Chapter three** will be presented to PECBMS and discussions surrounding the potential use of the "direct" European and regional indicators will take place.

6.7 Future research

This research explored the development of an updated European Forest Bird Indicator using site-level data available for the 168 common European breeding birds. This was due to the fact that PECBMS only produces population indices for this set of species as they produce reliable, long-term estimates of population changes. However, methods are now available to produce reliable population indices for rarer, less abundant species (Korner-Nievergelt *et al*., 2022), therefore, future research should explore the development of European bird indicators using the niche-based framework and site-level data from all breeding bird species in Europe. This would potentially allow even more sensitive species to be included in the indicator.

Although this thesis focused on the development of avian indicators in forest using the niche-based framework, future studies should consider using this framework to develop avian indicators in other habitats, or indicators for other taxa. For example, there is the potential to explore the development of an updated European Farmland Bird Indicator using this method to complement the updated European Forest Bird Indicator. Additionally, given the importance of invertebrate species to fulfil vital ecosystem services such as pollination, pest control, nutrient cycling and natural products and sensitivity to environmental changes (Prather *et al*., 2013), there is a need to explore the development of a niche-based invertebrate indicator.

This thesis explored large-scale temporal and spatial patterns in functional diversity for species subsets within forest and farmland habitats and based on the results, provided suggestions as to the potential underlying environmental drivers for these patterns. However, widespread information on long-term changes in temperature, rainfall, management practices, habitat and location and size of protected areas could be used to more closely explore the drivers of temporal and spatial patterns in functional diversity indices of species subsets. Additionally, it would be intriguing to explore the relative influence each species has on shaping the functional structure of generalists, specialist and visitor communities (Basile, 2022). Correlating each species functional importance with environmental drivers would shed further light on how specific environmental conditions influence community composition and species' relative abundances.

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