From local to global: biodiversity estimation and implications



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ABSTRACT

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Biodiversity describes the variety of life from genes to species and ecosystems, providing essential ecosystem services for humans. However, global biodiversity is in peril due to unsustainable human appropriation of ecosystem products and ecosystem transformations to other utilisations. Meanwhile, due to complex spatial patterns and highly dynamic changes, data describing and explaining biodiversity are also heterogeneous. Studies that used longitudinal and cross-sectional data to investigate global diversity change sometimes draw divergent inferences. This suggests an urgent need for helpful diversity estimation to account for the complex interactions amongst species, humans, and natural and built environments. In this thesis, I focus on spatial sample coverage, scale, structure and human-nature interaction that may influence diversity estimation. I also demonstrate that proper diversity estimates are essential for evidence-based conservation by testing whether conservation translocation (i.e., rewilding) can fill native functional gaps effectively.

First (Chapter2), based on neutral community models, I demonstrate that spatial sampling coverage and scales can reconcile divergent inferences on global diversity trends. I show that estimated diversity trends in a landscape with declined diversity can be both increased and decreased in the case where spatial sampling coverage is small, and the local survey scale is imprecise. Next (Chapter 3), I analyse the spatial distribution of diversity time-series recognised as having similar behaviours in temporal variation. I find that spatial diversity patterns can be independent of geographic structure if incorporating information of continued diversity change in the past. Expanding to a perspective of longitudinal analyses (Chapter 4), I illustrate that survey behaviours may respond differently to habitat change during long-term biological survey programmes. I find a significant proportion of survey cessations were associated with habitat change. As habitat change often causes diversity loss, this implies a failure in recording decreased diversity in studies estimating temporal diversity trends. Finally (Chapter 5), I shift to a conservation context and contrast rewilding with three other processes that influence native diversity. I show that effects of different processes vary much in infilling or expanding native functional space and functional diversity change caused by rewilding species are idiosyncratic.

Overall, this thesis contributes to elucidating the relationship between actual and estimated nature across scales, notably in diversity estimates. It also demonstrates how spatial structure, scale, and community history may influence estimated diversity patterns and the direct causal implications for shaping conservation strategies. Together, these findings form a foundation for expanding our understanding of the ecological implications of diversity estimation and the mechanisms underpinning this (Chapter 6).

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AUTHOR CONTRIBUTIONS

Main contributors

Wenyuan Zhang had independent intellectual input into all aspects of the thesis. He collected and analysed the data for all studies, drafted chapters, and incorporated co-author comments to produce final manuscripts for each chapter.

Ben C. Sheldon (supervisor and co-author of all data chapters) provided intellectual input, guidance, and feedback.

Richard Grenyer (supervisor and co-author of all data chapters) provided intellectual input, guidance, and feedback.

Kevin J. Gaston (supervisor and co-author of all data chapters) provided intellectual input, guidance, and feedback.

Further author contributions information accompanies each chapter.

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1

Introduction

"The most striking feature of Earth is the existence of life, and the most striking feature of life is its diversity."

– David Tilman (2000)

Introduction

Biodiversity describes the variety and heterogeneity of organisms at all levels of the hierarchy of life, from genes to species, to ecosystems (Gaston, 2000). For centuries, biodiversity with its mesmerising beauty, especially the spectacular ways in which novel life forms have diversified and assembled into intricate communities and ecosystems over uneven distributions, has intrigued generations of natural historians, paleobiologists and ecologists. Although most species on Earth – at the time of writing – remain uncharacterised and the number of catalogued species represents only a fraction of the total found in nature (Costello *et al.*, 2013; Moura & Jetz, 2021), we cannot ignore the fact that the remarkable biodiversity shapes and defines life on our planet, and that biodiversity provides crucial ecosystem functions for human beings (Mace *et al.*, 2012). This important role of biodiversity is embodied not only in providing goods directly and regulating ecosystem processes (e.g., crop and livestock, clean air and water, pollination, pest control), but also in the cultural values *per se*, including recreation, tourism, aesthetic enjoyment, inspiration and education values (Gaston & Spicer, 2004; Turner *et al.*, 2007; Hooper *et al.*, 2012; Tilman *et al.*, 2014).

Nevertheless, biodiversity is undergoing fundamental alteration under rapidly increasing pressures of global change (Newbold *et al.*, 2015; Rosenberg *et al.*, 2019; Leclère *et al.*, 2020). To provide the evidence base to underpin conservation initiatives for global biodiversity, it is essential to understand how biodiversity responds to established and emerging challenges from multiple perspectives. The way we have recognised and

addressed this fundamental knowledge gap has much relied on studies of biodiversity estimation, which derive conclusions from approaches that use data collected from specimens and local biological observations (Worm & Tittensor, 2018). This can introduce biases towards our understanding of biodiversity when locally surveyed diversity is incapable of providing adequate information to capture diversity at large scales (Beck *et al.*, 2014; Desquilbet *et al.*, 2021; Welti *et al.*, 2021). Knowledge of the complex interactions amongst individuals, populations, species, natural and built environments, and human activities, is therefore vitally important to bridge the gap between the true diversity in nature and the estimates made. This is particularly important for studies in an effort to describe and explain macroscale diversity patterns using biological survey data and environmental variables at local scales. However, despite centuries of human fascination with biodiversity and conservation efforts, we lack important comprehension of linkages of biodiversity estimation between local and global scales.

Measures of biodiversity

Measures of biodiversity comprise two fundamental dimensions. The first is exploring different forms of diversity and their ecological implications. Historically, most of the emphasis has concentrated on 'taxonomic' diversity, which is the diversity in identities of species, classified, for example, by a Linnaean taxonomy that uses a binomial nomenclature for naming taxa (Hill *et al.*, 2016; Santini *et al.*, 2017). Charles Darwin's 1855 survey of plants in Great Puckland's meadow, a 13-acre hayfield close to his house in Kent, south of England, is probably the first recognised quantification of biodiversity,

where biodiversity is defined as the taxa that co-occur at a given place and time (Costa, 2017). However, it was not until the 20th century that the formation of a Central Committee for the Study of British Vegetation in 1904 represented the first significant attempt at coordinating biodiversity surveys; this led directly to the establishment of the British Ecological Society in 1913 (Berry, 1988). Systematic biodiversity surveys then became commonplace in the 20th century and made the formal estimation of biodiversity change possible. These surveys and datasets have intrigued a deluge of explorations into biodiversity patterns and underlying mechanisms, such as debate over the biological species concept (Wheeler & Meier, 2000; de Queiroz, 2005), the theory of island biogeography (MacArthur & Wilson, 1967), ecological niche theory (Chase & Leibold, 2009; Pocheville, 2015) and neutral theory in macroecology (Hubbell, 1997; Bell, 2001; Hubbell, 2001), which remain active research fronts today.

However, those studies that focused on taxonomic diversity ignore the effects of functional or evolutionary characteristics of species (Vane-Wright *et al.*, 1991; Faith, 1992; Petchey & Gaston, 2006). This is because species are not all equivalent, some performing more complicated functions and some clades carrying more evolutionary history than others (Vane-Wright *et al.*, 1991; Tilman, 2001; Cadotte & Davies, 2010; Purvis *et al.*, 2011). To account for these facets of diversity, functional and phylogenetic diversity measures have been developed in the 21st century (See review in Flynn *et al.*, 2011; Pavoine & Bonsall, 2011). Indeed, many studies have shown that species perform different functions in an ecosystem (Hooper *et al.*, 2005) and can be characterised by their functional traits, i.e. the morphological, physiological, or behavioural characteristics

which also impact the species fitness via their influence on growth, reproduction and survival (Petchey & Gaston, 2006; Violle *et al.*, 2007). For example, suppose a species from a particular community was replaced by an 'equivalent' species belonging to the same functional group. In that case, the impact on the community and landscape structure or ecosystem functioning is likely to be minimal, compared to the replacement by species belonging to different functional groups (Walker, 1992; Rosenfeld, 2002; Flynn *et al.*, 2009). In addition, there is growing recognition that the branching pattern on a phylogenetic tree reflects the accumulation of phenotypic, genetic, behavioural, and/or phenological differences between evolutionary lineages (Tucker *et al.*, 2017). Measures of phylogenetic diversity are now widely used to help understand patterns of biodiversity (Winter *et al.*, 2013; Brooks *et al.*, 2015) or the potential functioning of ecosystems, although the explicit relationship between functional and phylogenetic diversity remains unclear (Lavergne *et al.*, 2010; Mouquet *et al.*, 2012; Cadotte *et al.*, 2017).

Apart from different forms of diversity, the second fundamental dimension of biodiversity measures is investigating shifts in species composition. This is because whilst different communities may have a similar number of species and comparable species abundance distributions, they can contain different species assemblages. An analysis that ignores species composition can miss essential differences, such as variation in numbers of native or specialist taxa. Whittaker (1960) and Whittaker (1972) described two complementary facets of biodiversity as alpha (α) and beta (β) diversity, with alpha diversity referring to the 'level' of diversity (such as species richness - the number of species found within a defined region at a given time), and beta diversity as compositional differences between

these study units of alpha diversity. He further stated that gamma (γ) diversity is the overall diversity of the broader landscape within which alpha and beta diversity are measured. These perspectives of alpha, beta and gamma diversity can also be applied in estimating functional and phylogenetic diversity, for example, quantifying richness of phylogenetic trees or traits, and in evaluating the difference or divergence between sites (beta diversity) in either of the two facets of diversity (Cardoso *et al.*, 2014; Arnan *et al.*, 2017).

Coming into the 21st century, metrics and indicators continue to proliferate in order to capture the complex structure in, and values derived from, biodiversity. The increasing number of different metrics, however, can confuse how the different metrics relate to each other in both mathematical and ecological terms (Jarzyna & Jetz, 2016; Tucker *et al.*, 2017; Pascual *et al.*, 2021; Soto-Navarro *et al.*, 2021). In this thesis, I focused on taxonomic, functional and phylogenetic diversity to obtain a more comprehensive understanding of pluralistic facets of biodiversity estimation, and to not obfuscate conservation initiatives.

Estimation of spatial patterns

Understanding the prominent spatial patterns of biodiversity represents one of the most fundamental questions in ecology. Even to a casual observer, it is apparent that certain regions of the globe host a disproportionally large fraction of biodiversity. For many taxonomic groups surveyed in the terrestrial realm, including plants, vertebrates, and insects, species richness peaks in the wet, warm tropics and falls off steeply towards

higher latitudes and altitudes, alongside the change of species composition in spatially complex ways (Gaston, 2000). However, attempts to understand the distribution of biodiversity have mainly concentrated on identifying patterns in spatial gradients of species richness that transcend this complexity and the mechanisms that have triggered these patterns (Gaston & Spicer, 2004; Chase *et al.*, 2019). Inevitably, such efforts have primarily concerned the small number of better-known taxa, especially plants, birds and mammals on the land of low elevation, and molluscs and fish in oceans of shallow water (Mora *et al.*, 2008; Meyer *et al.*, 2016; Daru *et al.*, 2018; Davis *et al.*, 2021). Very little empirical information is available about the spatial biodiversity patterns in most of the highly speciose groups (e.g., the bacteria, fungi and insects), or in the high-elevation land areas and deep ocean environments (Hughes *et al.*, 2021). For no geographic area, even if only of moderate size, have we as yet completely quantified all of the species (across all taxa) that are present. The ability to estimate and understand spatial patterns of biodiversity is limited by current knowledge of biases underlying accessible data. Therefore, it is important to explore how those biases may influence our understanding of biodiversity patterns and what insights we can gain from them.

Debate on temporal trends

Species extinctions are believed to occur much faster than the background rate estimated from the fossil records due to human activity (Barnosky *et al.*, 2011; Pimm *et al.*, 2014; Davis *et al.*, 2018). Nonetheless, recent analyses based on time-series datasets of biodiversity argue that local species richness in terrestrial assemblages is not in decline across the planet (Vellend *et al.*, 2013; Dornelas *et al.*, 2014; McGill *et al.*, 2015; Vellend

et al., 2017; Blowes *et al.*, 2019). The claim that local diversity is not in decline originates primarily from analysis of time-series data that have been collated from biological survey programmes using repeated measurements of biodiversity at individual locations around the planet (Dornelas *et al.*, 2014; Hillebrand *et al.*, 2018; Blowes *et al.*, 2019; Antão *et al.*, 2020). Whilst these analyses have confirmed substantial turnover in species composition across locations, and across time at single sites, they have found no evidence of systematic declines in species richness at local scales. Instead, these data syntheses have shown that species richness decreased in some locations, whereas it increased in others (Gonzalez *et al.*, 2016). These opposing trends have been offsetting such that there has been no net change in species richness, and suggested this pattern is globally representative of biodiversity change at local scales (Cardinale *et al.*, 2018).

Since the unexpected results and the publications in high-profile journals, data syntheses like those have sparked considerable scientific debate on the generality of biodiversity trends across the globe (Cardinale *et al.*, 2018). This also implies a critically important influence on the field of conservation biology. If, as studies of time-series datasets suggested, local-scale species richness is not generally declining as has long been presumed, historical means used for biodiversity conservation may need to be revised, and biodiversity trends reported in many textbooks may need to be rewritten.

In contrast, opposite conclusions have stemmed from analyses that focused on estimating diversity change using spatial comparisons in which measures of species diversity in sites that are disturbed by human activities are compared to those in undisturbed reference sites

(Aronson *et al.*, 2014; Newbold *et al.*, 2016; Moreno-Mateos *et al.*, 2017; Jung *et al.*, 2019). These analyses usually collated data from published studies to compare biodiversity from sites that vary in the nature or intensity of human modification in relation to land use (Hudson *et al.*, 2017). Studies that have adopted spatial comparisons to contrast human-disturbed sites to reference sites have corroborated the historical view that local diversity is declining, but the magnitude of decline differs with the type and severity of anthropogenic impacts (Aronson *et al.*, 2014; Murphy & Romanuk, 2014; Newbold *et al.*, 2015; Newbold *et al.*, 2016; Moreno-Mateos *et al.*, 2017; Rosenberg *et al.*, 2019).

To resolve the debate, research has been carried out aiming to demonstrate different types of biases underlying sampling schemes of both approaches that may have generated the divergent results, e.g., lack of historical baselines (Gonzalez *et al.*, 2016) and ignoring the complex sampling history inherent to different long-term monitoring programmes (Welti *et al.*, 2021). However, to allow broader conclusions about biodiversity change, there is still a need to understand the extent to which we may reconcile these divergent inferences.

Challenges in a changing world

Humans exert an outsized influence on ecosystems in the Anthropocene, and every species has to contend with the growing pressure of global change (Barnosky *et al.*, 2011; Waters *et al.*, 2016). This also poses a diverse array of challenges in the way of estimating and understanding biodiversity in a changing world, which can be viewed from three

facets. First, distribution and composition of global diversity have been changing much faster than ever owing to accelerating rates of human modification of natural environments (Hull *et al.*, 2015; Isbell *et al.*, 2017). An effective biodiversity estimate demands considerable time and effort through a variety of processes, ranging from sampling scheme design to data collection, organisation and analysis. It is therefore challenging to develop broad approaches in attempts to collect and analyse biological information rapidly and make helpful estimates of diversity before it changes too distinctly. In fact, although some novel approaches, such as environmental DNA that collects genomic DNA from organisms detected in an environmental sample to acquire taxonomic information, have been proposed for rapid collection of biological information (Taberlet *et al.*, 2012), efforts are still needed to test whether these approaches can capture biodiversity effectively compared to classic biological surveys (Cilleros *et al.*, 2019; Burki *et al.*, 2021; Lyet *et al.*, 2021). This is also the case for other new technological innovations, including sampling of remote sensing, networks of camera traps and sensors, and acoustic surveys, which have the potential to automate sampling and analyses. Therefore, from a methodological perspective, a non-trivial challenge may be to continue increasing spatial coverage of existing long-term biodiversity surveys and to develop new approaches to interpret diversity patterns from them.

Second, complexity arises at all genetic, species and ecosystem levels of biological community organisations, making it difficult to get a comprehensive understanding of biodiversity rather than focusing on one or several aspects of it. With the widespread recognition of the importance of multidimensionality in biodiversity, frameworks have

been proposed to measure and assess more pluralistic perspectives on biodiversity, but there is little consensus on their relative merit (Pascual *et al.*, 2021; Soto-Navarro *et al.*, 2021). This is mainly because knowledge is required in a form that matches the specific needs of policymakers, land managers and environmental educators who work with the biodiversity concept, whilst their needs in diversity estimation often vary with each other. Therefore, diversity facets included in the proposed frameworks also differ a lot (Soto-Navarro *et al.*, 2021; Taylor *et al.*, 2021).

Third, biases of human observers influence our understanding of the characteristics of natural systems. As stated above, biodiversity estimation depends on a range of different processes, and each of them can hugely bias the outcome. This has resulted in gaps between actual and estimated diversity patterns, presenting challenges for diversity estimation. On the one hand, sampling schemes that followed a process of imperfect top-down design sometimes overlooked the difference in local environments (Gotelli & Colwell, 2001; Bosch *et al.*, 2017). It is thus challenging to investigate how the complex local heterogeneity may bias sampling design and diversity estimation in the absence of information on local environments (Thuiller *et al.*, 2019; Desquilbet *et al.*, 2021; Welti *et al.*, 2021). On the other hand, it is difficult to predict how local surveyors interact with natural environments and to evaluate the effects on diversity estimation caused by changes in survey behaviours. For example, habitat loss can lead to a record of dramatic population decline for given species, but the declining record may also be attributed to the loss of interest of surveyors. If these two factors were not distinguished, the corresponding biodiversity estimation would be biased. Therefore, detecting the influence

of survey behaviour on diversity estimation becomes increasingly crucial in the context of global ecological change. Indeed, personalised ecology has been proposed to emphasise the interactions between individual people and nature and their ecological dimensions, especially factors that can influence such interactions (Gaston *et al.*, 2018; Gaston, 2020; Soga & Gaston, 2020). Just as human-nature interactions can no longer be uncoupled from a full understanding of the ecological foundations, it is no longer possible to construct sound ecological science without explicit attention to the interactions between people and nature as a key determinant of how much reality we can obtain from the ecological world.

Aims and objectives

The overall aim of my research is to explore the extent to which observed diversity patterns at local scales can signal diversity at larger scales and their implications for biodiversity conservation practices. In a larger context, I aim to reveal underlying mechanisms amongst multiple dimensions of biodiversity estimation, and, importantly, provides insights for the understanding of the relationship between observed and actual biodiversity patterns, so that governments, conservation policymakers, and managers can design, implement and maintain equitable, socially acceptable and sustainable conservation strategies that both protect nature and benefit human society. Using simulation modelling and biological records of birds and mammals, the main objectives are to:

1. Explore diversity estimates under scenarios of different spatial sample coverages and scales on virtual landscapes, and test whether they can reconcile divergent inferences on global diversity change.
2. Test whether geographic structure should be used as a default rule to delimit patterns on diversity change, i.e., ask whether diversity time-series that have similar behaviours in the temporal variability are geographically structured.
3. Understand the interactions between environmental change and survey behaviours, and how the interactions may influence estimation of long-term biodiversity trends.
4. Investigate the ecological justifications of a procedure of conservation translocation, i.e., rewilding, that aims at restoring ecological functions by reintroducing extirpated species, assessing whether they can support an effective conservation initiative.
5. Discuss and identify how insights feed across different strands of the work, with the aim of highlighting the hierarchy in diversity estimation to enhance the understanding of biodiversity and provide novel insights for biodiversity conservation.

Geographic and taxonomic scope

Like so many macroecological analyses, this thesis connects disparate regions of the world. I focus on estimating and understanding the biodiversity patterns in areas of the Northern Hemisphere i.e., North America and the United Kingdom, as well as simulated virtual landscapes. In North America, I study factors that may influence biodiversity

estimation for birds in the terrestrial realm, given that birds are the most documented group of species and can underpin the multiple objectives of my research. Aside from birds, I incorporate terrestrial mammals for analyses in the United Kingdom towards a broader conservation scope.

Thesis outline

In this thesis, I investigate different factors that may impact estimation of multiple facets of biodiversity from local to global scales, comprising five chapters. Spatial sample coverage and scale are critical for biodiversity estimation. Although much work has focused on biases in global biodiversity patterns relating to taxonomy, accessibility, ecotype and data type (Hughes *et al.*, 2021), the specific role of spatial coverage and scale in determining biodiversity estimation is much less studied. However, given the increasing number of studies that try to reach conclusions about global diversity patterns using relatively limited and biased datasets (Thuiller *et al.*, 2019; Hughes *et al.*, 2021; Pascual *et al.*, 2021; Welti *et al.*, 2021), it is necessary to examine the extent to which spatial sample coverage and scale can reconcile divergent inferences on whether local diversity is in decline across the planet. Therefore, in **Chapter 2**, I evaluate the effects of spatial sample coverage and scale on estimating global diversity change. I construct virtual landscapes to simulate the community change based on neutral community modelling approaches. I demonstrate the effects of spatial sample coverage and scale on biodiversity estimation by contrasting diversity trends across different sampling areas and scenarios of varied spatial scales. I show that even with random sampling design, limited sampling coverages can result in biased increasing or stable diversity trends. This work

also presents how spatial sample coverage can influence diversity estimation at different spatial scales and highlights their potential to reconcile divergent inferences on global diversity change.

Whilst biodiversity trend is a useful indicator for assessing the effectiveness of conservation policies and informing allocation of conservation resources (Ferraro & Pattanayak, 2006; Rodrigues & Brooks, 2007; Saout *et al.*, 2013), they are sometimes neglected in recognising diversity patterns. To this aim, in **Chapter 3**, I propose a framework to ask whether the diversity distribution is geographically structured if incorporating the behaviour of diversity change in the past. I first recognise diversity patterns based on behaviours of time-series independently of the relative or absolute geographic locations. Thus, time-series of similar changes in diversity, rather than of close geographic distance, are grouped into the same pattern. Further, I test whether the locations of diversity time-series that have the same pattern are geographically structured or randomly distributed in space. I find strong support that avian diversity time-series in the same pattern are randomly distributed across North America. This implies potential biases in studies of diversity trend estimation based on geographic structure *a priori*. Therefore, I suggest that approaches considering diversity variability independently of geographic structure can support directions for organising rules of biodiversity time series.

Interactions between humans and nature, especially human behavioural responses to natural environment changes, are crucial to biodiversity estimation. In **Chapter 4**, using North American Breeding Bird Survey data and remote sensing data for land cover

change, I demonstrate that habitat change can be associated with survey cessations in long-term biodiversity monitoring programmes, whilst these survey cessations can lead to failures in recording the diversity loss caused by habitat changes. Therefore, biodiversity loss can be underestimated in studies using long-term time-series to estimate diversity trends. I argue that researchers and conservation practitioners should be aware of the potential for bias in such data and seek methods that are more robust in evaluating biodiversity trends and making conservation decisions. In addition, how species vary with their responses to environmental change is also important for diversity estimation. In a series of appendices, I include some work that I contributed to that explores predictors of diversity in East Asian waterfowl, showing (i) responses of migration birds to habitat degradation in the East Asia Flyway differ in their seasonal distributions, where species with broader migration corridors are less likely to be affected by habitat degradation (**Appendix D)**; (ii) wintering geese in China have failed to capitalise on farmlands primarily because of the intensive human disturbances (**Appendix E**); (iii) waterbird diversity alongside Yangtze River Floodplain is impacted not only by the habitat that they commonly utilised but also by the surrounding landscapes that they rarely utilised (**Appendix F**).

In **Chapter 5**, I move to examine the ecological justifications of conservation programmes, i.e., rewilding, that aims to restore local ecological functions by reintroducing extirpated species that once existed in given areas. I separate out the effects of rewilding on native diversity by contrasting the diversity change after adding rewilding species to extant native species pool to that of adding introduced, naturalised and naturally

colonised and extirpated bird and mammal species in the United Kingdom. I evaluate the functional overlaps between native species and other groups of species using a hypervolume analysis. I show that (i) introduced/naturalised birds increase the most functional uniqueness to native functional space, (ii) functional diversity change caused by rewilding species is largely influenced by the inclusion of specific species, and (iii) rewilding mammals contribute the least functional uniqueness to native functional space. The results imply that overall rewilding programmes are not particularly effective in expanding or infilling native functional trait space, and, if doing so is a principal aim, the ecological justification of rewilding programmes may need reassessment.

Ultimately, I end the thesis with a discussion (**Chapter 6**) of the findings made throughout this work and their relationships to one another. I synthesise the primary findings to illustrate how the work has contributed to understanding the interplay between diversity estimation and human activities, and provide novel insights into conservation policies based on biodiversity estimation. Additionally, I comment on the potential utility of furthering our understanding of diversity estimation for various practical applications, such as biodiversity conservation. Finally, I highlight several outstanding questions, and discuss how the advancements made within this thesis now provide a foundation to tackle various unresolved challenges. This is mainly in reference to examining the interaction between changes of natural environments, survey behaviours and diversity estimation, as well as the mechanisms underpinning this, in hopes of elucidating their ecological and conservation implications.

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2

Reconciling divergent inferences on global diversity change

Estimates of local biodiversity trend depend on spatial sample coverage and scale

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Statement of authorship

W.Z. and K.J.G. conceived the ideas and all authors contributed critically to the methodology design. W.Z. performed the analyses and led the writing of the manuscript. All authors contributed to drafts of the manuscript.

Data accessibility statement

No new data were used in the analyses.

Abstract

Different approaches have drawn contrasting conclusions on whether local diversity is declining across the planet. It is critically important to investigate mechanisms that may cause those divergent inferences and whether they can be reconciled. Here, based on simulating 40,000 time-series of diversity change on a spatially neutral landscape, we test what local diversity trends can arise when global diversity declines, considering the effects of spatial sample coverage, intensity and spatial scales of local surveys. We show that, in a landscape with an overall declining diversity, local diversity trends estimated from time-series of different randomly selected sites (e.g., spanning 1% of the landscape coverage) can be both positive and negative. The trend is more likely to be biased when spatial sample coverage is smaller (i.e., no more than 10% of the total landscape) and fewer individuals are sampled. The probability of recording a biased positive trend can exceed 36% for scenarios where large-scale diversity is inadequately represented by small-scale surveys (undercoverage bias) or differences in community structures within a large-scale sampling area are ignored (imprecision bias) in local surveys. Our findings suggest that inadequate spatial sample coverages and biases in spatial scales of local diversity surveys could lead to divergent inferences on overall trends of local biodiversity.

Main text

Over the past few years, considerable debate on the generality of local biodiversity trends has arisen due to divergent conclusions derived from two distinct approaches to estimating those trends (Cardinale *et al.*, 2018). One involves spatial comparisons, in which measures of diversity in sites that are disturbed by human activities are compared to those in undisturbed reference sites. Such spatial comparisons have corroborated the historical view that local diversity is declining, but the magnitude differs by the type and severity of anthropogenic impacts (Aronson *et al.*, 2014; Murphy & Romanuk, 2014; Newbold *et al.*, 2015; Newbold *et al.*, 2016; Moreno-Mateos *et al.*, 2017; Rosenberg *et al.*, 2019). The second approach involves the analysis of time series data that have been collated from studies using repeated measurements of biodiversity at individual locations around the planet. While these analyses have confirmed substantial turnover in species composition across locations, and across time at single locations, they have found no evidence of systematic declines in species richness at local scales (Dornelas *et al.*, 2014; Hillebrand *et al.*, 2018; Blowes *et al.*, 2019; Antão *et al.*, 2020). Instead, these data syntheses have shown that species richness is decreasing in some locations, whereas it is increasing in others (Gonzalez *et al.*, 2016). Because the time series datasets are distributed across different areas and over multiple geographic structures (Dornelas *et al.*, 2014; Blowes *et al.*, 2019), the proliferation of such datasets and sometimes unexpected results have received considerable attention (McGill *et al.*, 2015; Newbold *et al.*, 2015; Vellend *et al.*, 2017; Cardinale *et al.*, 2018; Blowes *et al.*, 2019).

Most criticisms of studies that have not found evidence of systematic diversity decline have concentrated on pointing out potential biases and errors existing in longitudinal studies (Fournier *et al.*, 2019; Welti *et al.*, 2021; Zhang *et al.*, 2021). They have provided important insights into understanding how best to analyse time-series data and what criteria should be met before a time series should be included in longitudinal studies. However, the more fundamental questions of the mechanisms underlying the divergent findings from spatial and temporal comparisons, and the extent to which they can be reconciled, are not well understood. Here, we examine what local biodiversity trends can arise when global biodiversity is in decline, in terms of different spatial sample coverages, scales and sampling intensities of local surveys.

We use a spatial neutral community model to simulate species distribution and biodiversity change (Bell, 2001). We then estimate the capacity of various spatial sample coverages to capture global diversity change (i.e., temporal species richness and turnover) at different spatial scales and sampling intensities. Neutral models describe communities of trophically similar species typically occurring in sympatry and potentially competing for resources (Bell, 2001; Rosindell *et al.*, 2011). The diversity of the assemblage results from stochastic ecological processes acting on both local and regional scales (Hubbell & Lake, 2003). There are two assumptions in the neutral model (Bell, 2000; Hubbell, 2001). First, all individuals belonging to all species have the same probabilities of birth, death, and dispersal. This means that individuals exhibit no traits associated with their species identity that have any influence over their reproductive success, longevity, or movements. The absolute numbers of births, deaths and dispersal events will, however, vary between species, which will vary in abundance and distribution. Second, the community is

saturated with individuals, such that if one dies, another takes its place, and individuals are thus engaged in a 'zero-sum' game. From neutral theory, many observed properties and patterns in assemblage and community structure can be described and predicted, for example, species richness patterns, the form of species–abundance distributions, species-area relationships, and turnover in species composition with distance (Chave, 2004; Gaston & Chown, 2005; Wootton, 2005; Hu *et al.*, 2006; Jabot & Chave, 2009; Rosindell *et al.*, 2012). Therefore, considering both the ecological structuring of communities and sampling strategies are complex, we use neutral models as a simplified approach that retains much of the essentials of community processes to explore local diversity trend estimation considering effects of spatial sample coverage, scale and sampling intensity.

Our neutral community models – based on Bell's model (Bell, 2001; Bell, 2003; Bell, 2005) – are built on an artificial landscape of 200 × 200 sites, where individuals belonging to each of 250 species have the same probabilities of birth, death and dispersal. Each site has a carrying capacity of 2,000 individuals. There are two stages in our simulations (See methods for details). The first is constructing an initial landscape at dynamic equilibrium after 13,000 generations, where little change is observed in patterns of abundance and diversity (Figure S1). The second is simulating a changing landscape where overall diversity is declining. To achieve this, on the initial landscape, we switched off the immigration process from outside the landscape and randomly selected 5,000 sites whose carrying capacities were randomly reduced to 500 – 1,999 individuals. The carrying capacity of each site then remains constant for the rest of the simulations. In this way, diversity in our landscape will continuously decline until all species are extinct due to the stochastic extinction of rare species, combined with no speciation (Bell, 2000; Bell, 2001;

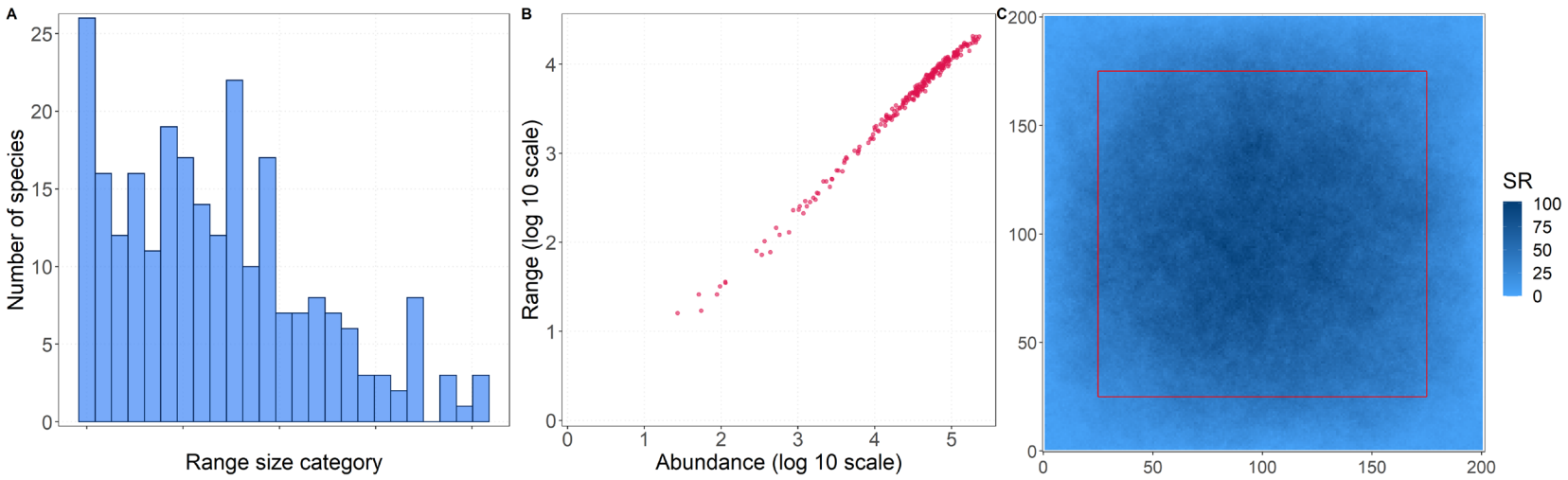

Figure 1. Neutral landscapes. Landscape structures for the initial landscape after 130,000 generations. The neutral landscape consisting of 250 species in the central 150 × 150 sites is analysed for local dispersal rate $u = 0.1$. **(A)** The distribution of range**.** **(B)** The range-abundance relationship. **(C)** The species richness distribution.

Gaston & Chown, 2005). We do not include processes like human interferences, which may cause abrupt diversity change (Jung *et al.*, 2019); thus, diversity trends in the neutral model are gradual.

We calculate diversity change in each site for the subsequent 500 generations on the changing landscape with diversity calculated once every five generations (100 data points), which generates 40,000 time-series of community change from all sites (the central 150 × 150 site time-series are used to reduce edge effects; Figure S1-C). We demonstrate the influence of spatial sample coverage on diversity estimation by calculating diversity trends from different numbers of randomly selected sites. To measure the effects of sampling intensity, we subsample the populations of a given site to model the number of observed individuals. The probability of detecting each species in that site is weighted to its population there. We then alter the number of observed individuals (subsampling level) in each spatial sample coverage and keep it constant between different generations and sites. We repeat the sampling process 1,000 times for each spatial sample coverage and sampling intensity.

Effects of sample coverage on capturing global diversity change

We estimate the long-term global trends in diversity in two ways: (1) overall trend – estimated by fitting a slope for all sampled diversity time-series and allowing each time-series to have a specific effect (i.e., varying intercepts); (2) average trend – measured by calculating the mean of slopes of each time-series allowing variance in both slopes and intercepts. We recorded a 5% species loss for the total 250 species in the whole landscape;

however, estimated local diversity trends varied under spatial sample coverages of no more than 25%. For an individual sample of time-series from randomly selected sites, the overall trend of species richness change can be either negative (Figure 1-A) or positive and stable (Figure 1-B) if the time-series are derived from sites spanning no more than 10% of the total area of the landscape. The overall diversity change trend is dependent on the proportion and extent of positive slopes of time-series at individual sites in that sample. The average trend for a 1% sample coverage can also be both statistically larger (Figure 1-A inset plot) and smaller (Figure 1-B inset plot) than zero.

The probability of observing a biased positive trend of global diversity change can be measured by the frequency of observing a positive trend in the 1,000-time samplings of each spatial sample coverage and sampling intensity. This is also largely impacted by spatial sample coverage: positive species richness trends are more likely to be observed in small sample coverages but are less likely in large sample coverages (Figure 1-C; Table S1). For example, the probability of observing a biased positive slope changes from 22.2% of 1% sample coverage to 3.8% of 5% sample coverage for 50 individuals observed each time. For the effects of sampling intensity, a larger number of observed individuals for a given spatial sample coverage contribute to a lower probability to observe a biased positive trend (Table S1).

In contrast to species richness, temporal species turnover as measured by the Jaccard and Morisita-Horn dissimilarity indices exhibits consistent long-term changes in all sample coverages (Figure S2 and S3). This is because we calculated the community similarity

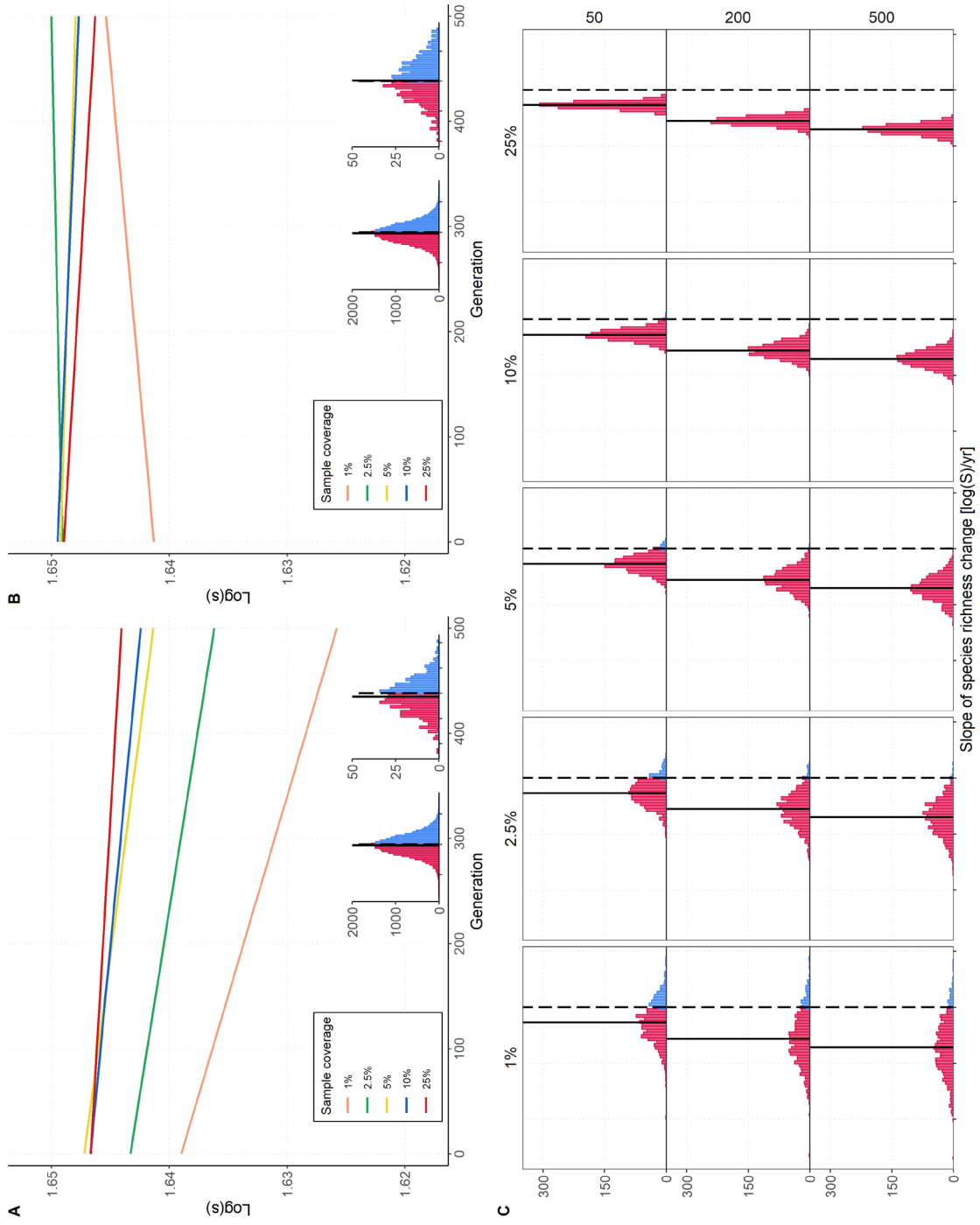
A
B
C
Log(s)
Generation
Sample coverage
1%
2.5%
5%
10%
25%
50
200
500
Slope of species richness change [log(S)/yr]

Figure 1. Effects of spatial sampling coverage. (A) (B) Examples show that in a landscape of overall diversity decline, the overall diversity (species richness) trends estimated from a single sample of time-series can be either positive or negative at sample coverages of no more than 10%, whereas diversity trends at the 25% sample coverage tend to be negative. Trend lines in different colours correspond to models in which a single slope but different intercepts were fitted to all time-series of that sample. Inset plots show the distributions of the slopes of each site at 100% (left) and 1% (right) sample coverages. The slope for each site is measured in a model where each time series could have different slopes and intercepts. **(C)** Distributions of overall trends for different samples of time-series across varied spatial sample coverages and numbers of individuals that were observed in each survey. Histograms are colour-coded as blue (positive slope) and red (negative slope). Solid lines represent the mean slope of 1,000 samples, and dotted lines are zeros.

Table S1. Probability to observe a biased positive trend for overall global diversity in different spatial sample coverages and spatial scales of local surveys.

Spatial sample coverage	Intensity		Undercoverage		Imprecision	
		Grain = 1	Grain = 4	Grain = 9	Grain = 4	Grain = 9
1%	50	22.2	36.7	37.2	42.6	44.4
1%	200	10.9	29.6	33.1	31.7	37.3
1%	500	7.3	25.6	30.5	25.9	32.7
2.5%	50	10.2	25.4	31.8	40.1	43.7
2.5%	200	2.9	16.2	26.0	20.4	30.6
2.5%	500	1.3	11.7	22.5	13.3	24.9
5%	50	3.8	20.9	30.1	34.6	45.1
5%	200	0.1	9.0	20.4	12.7	23.9
5%	500	0.0	5.6	15.5	5.9	15.1
10%	50	0.3	9.6	20.0	26.7	37.7
10%	200	0.0	2.2	8.7	4.6	15.6
10%	500	0.0	0.4	5.2	0.8	7.1
25%	50	0.0	1.7	7.6	14.4	31.0
25%	200	0.0	0.0	0.6	0.3	2.5
25%	500	0.0	0.0	0.4	0.0	0.4

between the first year of sampling (time-series baseline) and an ensuing year to detect cumulative changes in species composition. In this way, positive trends are indicative of accumulating changes associated with diverging community composition. Negative trends indicate time series at the earlier steps being more different from the baseline than later steps. These cases are rare in a neutral community, so we detect few negative species turnover trends across the landscape. The results indicate that for a landscape where overall species richness is declining and species turnover is occurring, the effect of spatial sample coverage on estimating temporal trends of species turnover is smaller than that of species richness.

Whether local species richness is declining globally is a hotly debated topic, and an important one, given both the scientific and social impacts that the conclusions pose (Cardinale *et al.*, 2018). We find the answer depends strongly on spatial sample coverage: in a landscape where the overall species richness is declining, small sample coverage is likely to see either a positive or negative trend, whilst larger sample coverage is more likely to see a negative one. When the sample coverage is small (no more than 10% of the total landscape), even if the sampling scheme is designed to be random, the outcome estimation is unlikely to provide helpful ecological information. Given that spatial sample coverage even for one of the most spatially and temporally extensive vertebrate trend datasets in the world (i.e., North American Breeding Bird Survey data) can be less than 0.4% of the continent's surface at a 1-km resolution (Veech *et al.*, 2017), inferences of global diversity trends may need careful reassessments.

We simulate and analyse diversity change in 500 generations, which suggests that the measured trend may be even more limited if in fact data have only been collected for smaller numbers of generations of monitoring schemes. Furthermore, models like ours that only simulate the gradual change of community structure ignore abrupt diversity change, which can also be important and generate stronger biases for diversity estimation. For example, habitat change can be associated with cessations in long-term biological monitoring programmes, which may result in failures to record the corresponding biodiversity loss, and in turn, biased diversity trend estimation (Zhang *et al.*, 2021). If this happens in smaller sample coverage where biased positive trends are already more likely to be observed, the probability of detecting a biased positive trend will increase. Adding abrupt diversity change in the simulation models, and incorporating effects of survey behaviours, will give a more complete picture of the capacity of local diversity to inform global diversity change.

Effects of spatial scales of local surveys

The spatial scales of local diversity surveys can be biased in two ways which will in turn bias the estimation of overall trends (Wang *et al.*, 2012; Zhang & Zhu, 2018). The first is a spatial undercoverage bias where a local biological survey is carried out at a small scale, and used to represent the diversity at a large scale. In this case, diversity trends in the unsurveyed areas are ignored. The second is a spatial imprecision bias where the local biological survey is conducted at a relatively large scale and diversity is surveyed across the whole area, but diversity variation between different parts of the area is not distinguished. To assess the effects of spatial scales of local surveys on diversity trend

estimations, we construct two scenarios to model the diversity measures: (1) undercoverage – diversity is surveyed at an individual site but is used to represent diversity at a larger grain size of four or nine sites (Figure 2); and (2) imprecision – diversity is surveyed at a grain size of four or nine sites between which the boundaries are removed, and diversity is measured as if they are one site (Figure 3).

Spatial undercoverage and imprecision in local surveys increase the probability of observing a biased positive trend for global diversity in all sample coverages and intensities. The effects become stronger when the grain size is larger (Figure 2 and 3). Using 2.5% spatial sample coverage and 200 observed individuals under the undercoverage scenario as an example, the probability of observing a biased positive trend increases from 16.2% to 26.0% when grain size increases from four sites to nine (Figure 3; Table S1), whereas this value for the grain size of one site is 2.9% (Figure 2). As for the same case of 200 individuals under the imprecision scenario, the probability for a biased positive trend increases from 13.3% to 24.9% when grain size increases from four sites to nine. Compared with the spatial undercoverage bias, the imprecision bias tends to have a less significant influence on biasing the global diversity estimation (Table S1).

Our analyses, based on sampling from neutral landscapes, indicate that the spatial scales of local diversity surveys can strongly influence the estimation in overall trends across such surveys. They can bias diversity trend analyses that used time-series data in two example scenarios. First, the undercoverage biases may occur for studies that used

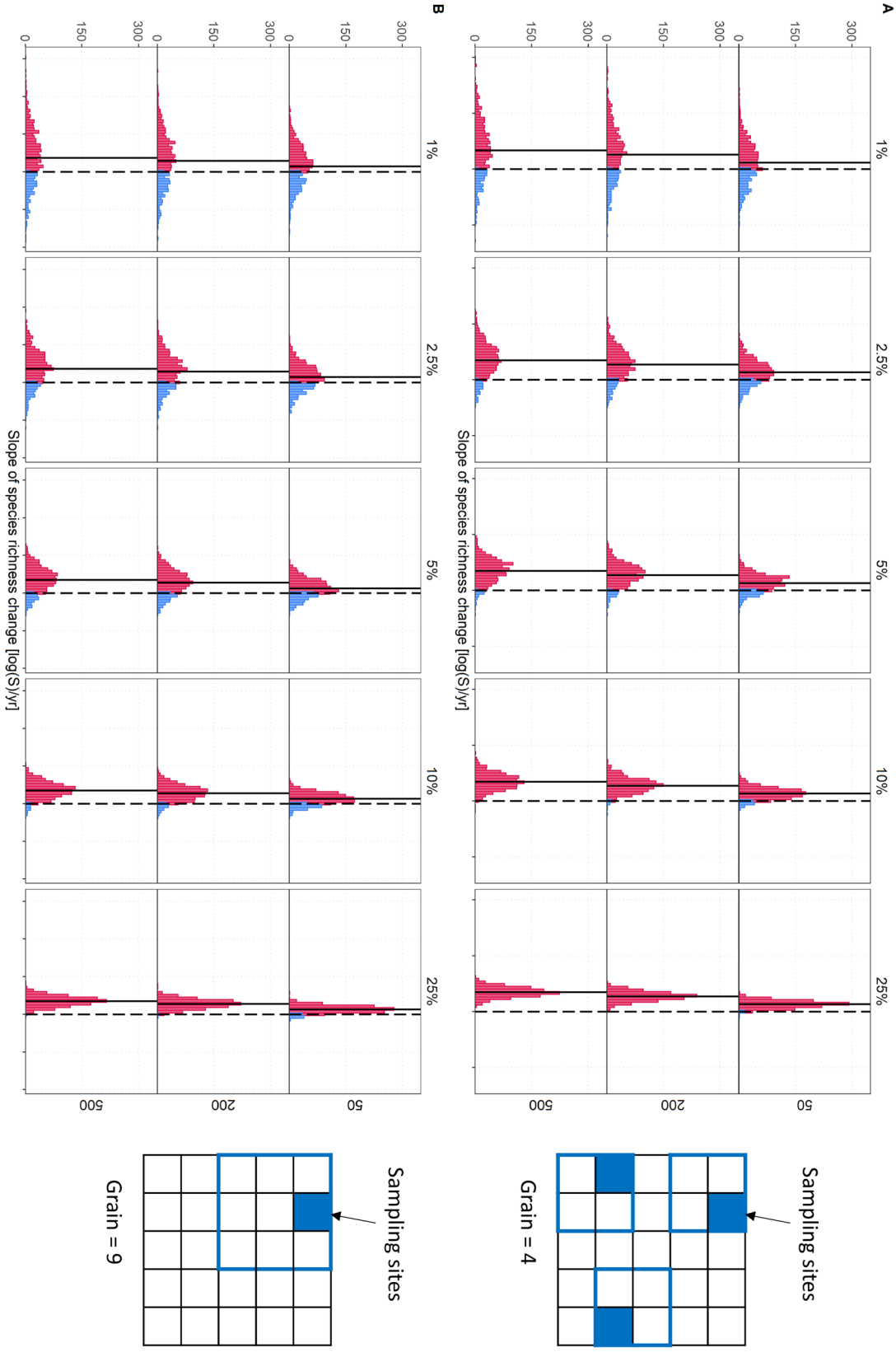
A
B
1%
2.5%
5%
10%
25%
50
200
500
0
150
300
Slope of species richness change [log(S)/yr]
Sampling sites
Grain = 4
Grain = 9

Figure 2. Effects of inadequate sample coverages in local surveys. Distributions of overall diversity (species richness) trends for different samples of time-series across varied spatial sample coverages and numbers of individuals that were observed in each survey for a grain size of four **(A)** and nine **(B)** sites. For each sample, one random site in the area of larger grain size was surveyed to represent the diversity of the whole area. Trend lines in different colours correspond to models in which a single slope but different intercepts were fitted to all time-series of that sample. Histograms are colour-coded as blue (positive slope) and red (negative slope). Solid lines represent the mean slope of 1,000 samples, and dotted lines are zeros.

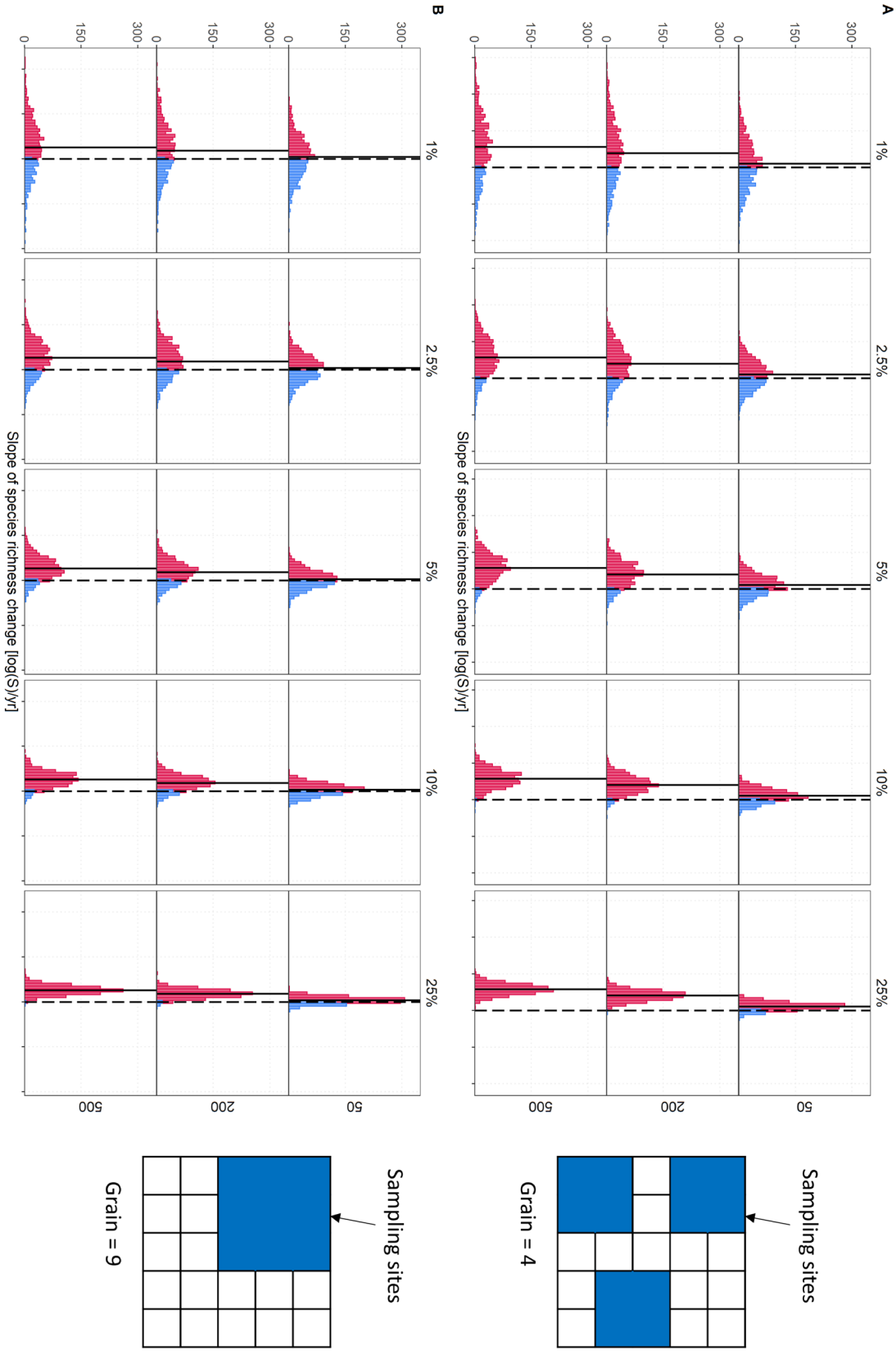
A
B
1%
2.5%
5%
10%
25%
50
200
500
0
150
300
Slope of species richness change [log(S)/yr]
Sampling sites
Grain = 4
Grain = 9

Figure 3. Effects of not distinguishing diversity trends in local surveys. Distributions of overall diversity (species richness) trends for different samples of time-series across varied spatial sample coverages and numbers of individuals that were observed in each survey for a grain size of four **(A)** and nine **(B)** sites. For each sample, all sites in the area of larger grain size were surveyed as a unit. Trend lines in different colours correspond to models in which a single slope but different intercepts were fitted to all time-series of that sample. Histograms are colour-coded as blue (positive slope) and red (negative slope). Solid lines represent the mean slope of 1,000 samples, and dotted lines are zeros.

longitudinal data from transect surveys (e.g., North American Breeding Bird Survey Pardieck *et al.*, 2020) and take the larger extent as the sampling area where the survey transect only traverses a part of it. Second, for synthesis studies that combined different datasets to analyse the global diversity trends at a dataset level (e.g., Dornelas *et al.* (2014)), differences in spatial extents of sampling were neglected, which may cause imprecision bias. In addition, owing to human interference with nature (Cardinale *et al.*, 2012; Hautier *et al.*, 2015; Newbold *et al.*, 2015; Thom *et al.*, 2017), diversity trends of different regions are often in practice more divergent than those in the neutral landscapes (Blowes *et al.*, 2019; Jung *et al.*, 2019). This implies a stronger undercoverage bias in practice than in neutral landscape. Due to imprecision biases, divergent local trends tend to have more significant offsetting effects on masking the diversity difference within that survey area. Therefore, the biases underlying analyses using time-series data in real nature can be even larger than those in the neutral landscape.

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Methods and materials

Neutral community construction

We use a spatially explicit, individual-based model, originally developed by (Bell, 2001; Bell, 2003; Bell, 2005). The behaviour of this model has been thoroughly described in the cited papers, particularly with respect to how well the resulting communities reproduce patterns found in empirical studies. Here, we simulate 250 species in an artificial landscape of 200 × 200 sites based on the neutral community model with spatial structure (Bell, 2000; Bell, 2003; Bell, 2005). The simulation comprises two stages. First, we construct an initial landscape with dynamic equilibrium when little change is observed in patterns of abundance and diversity. To achieve this, we assign 2,000 individuals (8 individuals for each of 250 species) to each site which is internally homogeneous and has an upper carrying capacity of 2,000 individuals. All individuals have the same birth and death probability of 0.5. Then at each time step, a newborn individual moves to a random neighbouring site with a probability of 0.1 and continues to move until it settles permanently in the site where it moved last. Newborns that disperse beyond the edges of the landscape are lost. After this, if the total number of individuals at any site is larger than the carrying capacity, individuals will be randomly removed to keep the community saturated. As is well-known, diversity in a neutral model landscape of this kind will continuously decline until all species are extinct due to stochastic extinction of rare species, combined with no speciation (Bell, 2000; Bell, 2001; Gaston & Chown, 2005). We thus set a 0.001 immigration probability for each species to keep our model from collapsing to a single species. This follows a 'normal configuration' of a neutral community in which one new immigrant of each species is introduced every few

generations, whilst each site is neither very isolated from its neighbour nor more or less completely connected with them (Bell, 2001).

Second, we simulate a landscape with continuous diversity decline by setting the immigration probability to zero and reducing the carrying capacity of 5,000 randomly selected sites. Specifically, we first randomly selected 5,000 sites, and then assigned them different carrying capacities that were randomly generated, ranging from 500 to 1,999. Thus, the immigration process is switched off on the initial landscape, and the overall diversity gradually declines. We then record the diversity change in each site for 500 generations on the landscape, with diversity metrics calculated every five generations (100 data points). This generates 40,000 time-series of each diversity metric from all sites. We retain the time-series of the central 150 × 150 sites to reduce edge effects. We used R packages 'neutral.vp', 'packfor' and 'permute' for the simulation.

Sampling scheme design

To quantify the effects of spatial sample coverage, sampling intensity, and spatial scale of local surveys on diversity trend estimation, we design our sampling scheme from three perspectives. First, for the spatial sample coverage, we alter the number of random-selected sampling sites whose total areas account for a varied percentage of the whole neutral landscape (i.e., 1%, 2.5%, 5%, 10%, and 25%).

Second, to measure the sampling intensity of species, we set different numbers of individuals to be observed in each sampling and model the probability of recording a given species to be proportional to its population at the survey site. Specifically, we subsample populations for different numbers of individuals (i.e., 50, 200 and 500) for different spatial sample coverages and keep it constant between generations and sites. We set the probability to record a given species weighted to its population in a given site.

Third, we contrast two scenarios to measure the effects of spatial scales of local survey sampling: (1) undercoverage – diversity is surveyed at an individual site but is used to represent the diversity at a larger grain size of four and nine sites, respectively (Figure 3); (2) imprecision – diversity is surveyed at a grain size of four or nine sites between which the boundaries are removed, and diversity are measured as in one site (Figure 4). We repeat each sampling of different sample coverage, sampling intensity, and scenarios of scales 1,000 times.

Diversity calculation

Although a plethora of diversity indices are available, species richness is one of the most fundamental and most straightforward ways to describe community and regional diversity (Magurran, 1988), and the variable – number of species – forms the basis of many ecological models of community structure (Connell, 1978; Gaston, 2000; MacArthur & Wilson, 2001). Species richness has also been the focus of the debate on whether diversity is declining across the planet (Cardinale *et al.*, 2018). Here, for each spatial sample coverage and each sampling intensity, we calculated the total species richness at every

generation. Apart from species richness, we also calculate the temporal species turnover to compare the composition of the individual local community through time. Specifically, we compute two metrics of species turnover: the Jaccard and the Morisita-Horn indices, both calculated using the function vegdist in 'vegan' (Oksanen *et al.*, 2020). We report the dissimilarity for each sample between the first and following generations in a time-series to measure the cumulative changes in the composition of local communities.

Analysis

We used two different approaches to estimate the long-term global trends in diversity of each metric. First, for the overall diversity trend, we fit a linear model with a single slope but a different intercept and a residual variance for each sample of time-series by using linear mixed-effect models (LMM). In this way, the model allows a specific effect for each time-series, and the overall trend is represented by the fitted slope. Second, we fit a linear model to time-series at each site that allows a different slope and an intercept by using ordinary least squares (OLS). The mean value of the slopes for a given sample thus measures the average diversity trend. To quantify the probability of observing a positive trend, we also analyse the frequency distributions of slope coefficients for each sample that is from different spatial sampling coverages, sampling intensities and scales in those 1,000-time sampling.

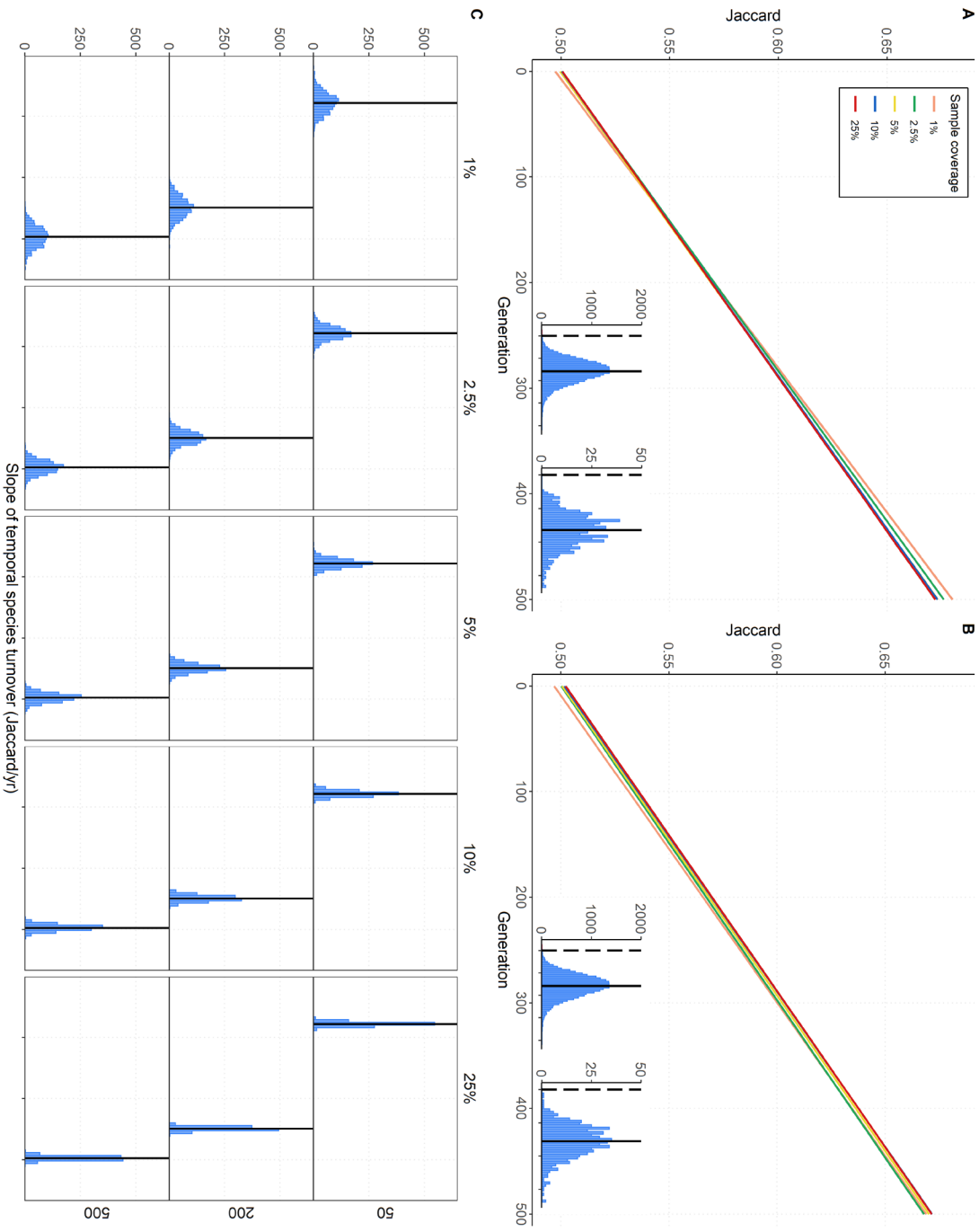
A
B
C
Jaccard
Generation
Sample coverage
1%
2.5%
5%
10%
25%
Slope of temporal species turnover (Jaccard/yr)
50
200
500

Figure S2. Effects of spatial sampling coverage on global species turnover estimation. **(A) (B)** Examples show that overall species turnover trends estimated from a single sample of time-series tend to be similar across spatial sample coverages. The species turnover is measured by the Jaccard dissimilarity index between a sample of each year and the initial year. Trend lines in different colours correspond to models in which a single slope but different intercepts were fitted to all time-series of that sample. Inset plots show the distributions of the slopes for each site at 100% (left) and 1% (right) sample coverages. The slope for each site is measured in a model where each time series could have a different slope and intercept. **(C)** Distributions of overall trends for different samples of time-series across varied spatial sample coverages and a various number of individuals that were observed in each survey. Histograms are colour-coded as blue (positive slope) and red (negative slope). Solid lines represent the mean slope of 1,000 samples, and dotted lines are zeros.

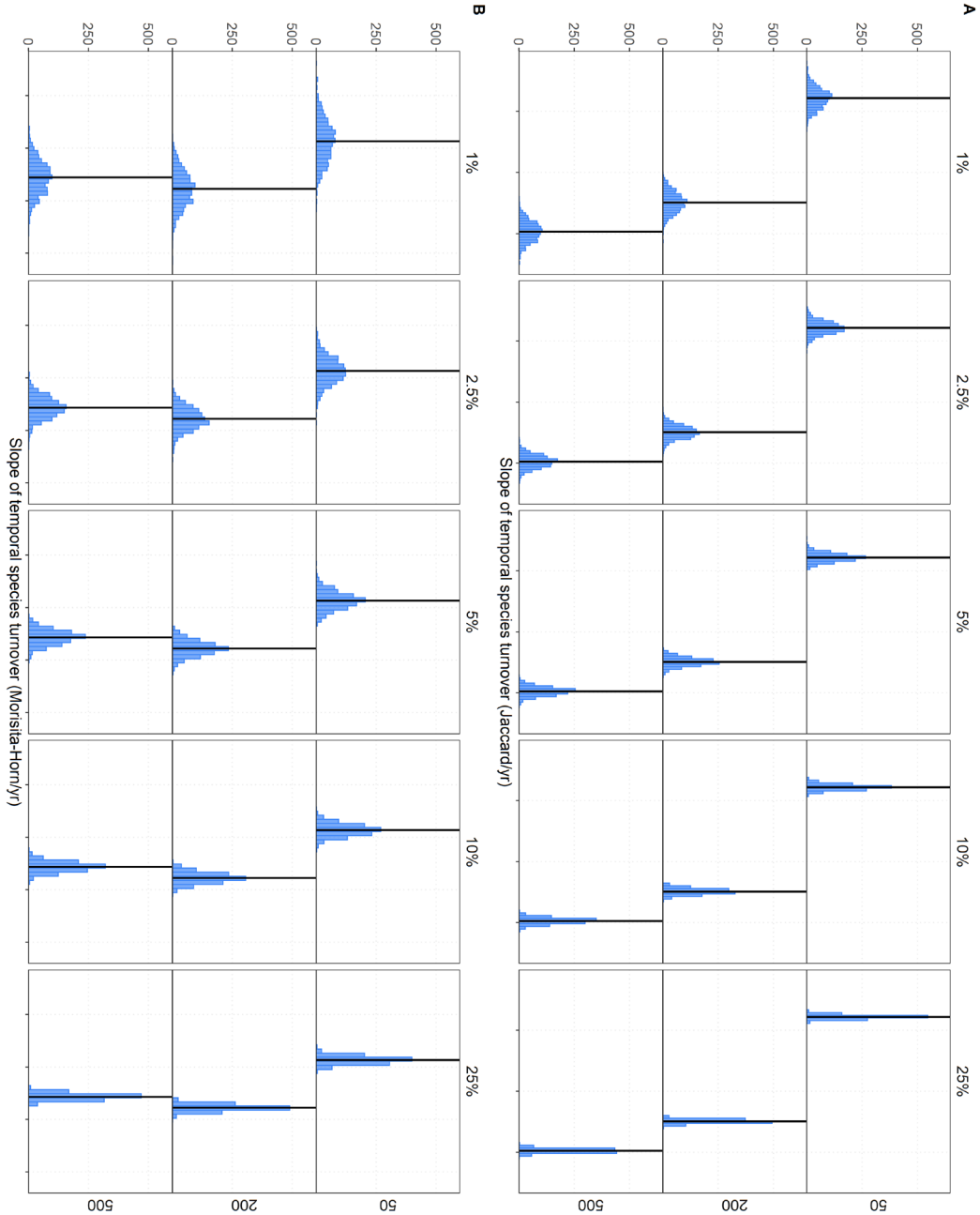
A
B
1%
2.5%
5%
10%
25%
50
200
500
0
250
500
Slope of temporal species turnover (Jaccard/yr)
Slope of temporal species turnover (Morisita-Horn/yr)

Figure S3. Effects of spatial sampling coverage on global species turnover estimation. **(A) (B)** Examples show that overall species turnover trends estimated from a single sample of time-series tend to be similar across spatial sample coverages. The species turnover is measured by Morisita-Horn similarity between a sample of each year and the initial year. Trend lines in different colours correspond to models in which a single slope but different intercepts were fitted to all time-series of that sample. Inset plots show the distributions of the slopes for each site at 100% (left) and 1% (right) sample coverages. The slope for each site is measured in a model where each time series could have a different slope and intercept. **(C)** Distributions of overall trends for different samples of time-series across varied spatial sample coverages and a various number of individuals that were observed in each survey. Histograms are colour-coded as blue (positive slope) and red (negative slope). Solid lines represent the mean slope of 1,000 samples, and dotted lines are zeros.

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3

Geographic bias in recognising diversity patterns

Challenging the geographic bias in recognising large-scale patterns of diversity change

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Abstract

Geographic structure is a fundamental organising principle in ecological and Earth sciences, and our planet is conceptually divided into distinct geographic clusters (e.g., ecoregions and biomes) demarcating unique diversity patterns. Given recent advances in technology and data availability, however, we ask whether geographically clustering diversity time-series should be the default framework to derive meaningful patterns of diversity change. To address this question, we first propose a framework that recognises patterns of diversity change based on similarities in the behaviour of diversity time-series, independent of their specific or relative spatial locations. Using over 0.9 million observations from the North American Breeding Birds Survey data, we then test whether time-series identified as having similar behaviour are geographically structured at all. We find little evidence of geographic structure in patterns of diversity change for North American breeding birds. Our results suggest that geographic proximity may not correspond to shared temporal trends in diversity; assuming that geographic clustering is the basis for analysis may bias diversity trend estimation. We suggest that approaches that consider variability independently of geographic structure can support directions for organising rules of biodiversity time series.

Keywords: pattern recognition, taxonomic diversity, functional diversity, phylogenetic diversity, spatial distribution, temporal trends, non-geographic patterns, biodiversity change

1 INTRODUCTION

Biodiversity describes the variety and heterogeneity of organisms at all levels of the hierarchy of life, from genes, species to ecosystems (Gaston, 2000). It is changing at accelerating rates worldwide due to human activity (Hull *et al.*, 2015; Pecl *et al.*, 2017). This implies an urgent need for appropriate assessments to explain the uneven distributions and patterns of biodiversity in order to decide conservation policies and gain maximal conservation benefits (Cardinale *et al.*, 2012; Jetz *et al.*, 2019). Most research attempting to describe and analyse the multiple dimensions of biodiversity has been from two perspectives. First, metrics and indicators are proliferating to capture different facets of, and values derived from, biodiversity. For example, taxonomic diversity has been assumed to function as a surrogate for different biodiversity facets, mainly owing to the easy quantification and interpretation of species distribution data. However, with the developing recognition that species are not equivalent (e.g., some perform unique functions and some clades carry more evolutionary history than others) (Vane-Wright *et al.*, 1991; Winter *et al.*, 2013), measures of functional and phylogenetic diversity have recently been developed (Winter *et al.*, 2013; Cadotte *et al.*, 2015) to incorporate these facets of diversity. To be more specific, functional diversity is a measurement that incorporates different functions that species perform in an ecosystem and is usually characterised in terms of functional traits, i.e. morphological, physiological, or behavioural characteristics (Petchey & Gaston, 2006). Phylogenetic diversity is a family of metrics derived from the phylogenetic distance among taxa and is sometimes controversially treated as a proxy for functional diversity, because functional traits are often phylogenetically conserved and measured imperfectly (Faith, 1992; Winter *et al.*,

2013; Cadotte *et al.*, 2017).

Second, studies have been conducted to investigate the spatial heterogeneity of biodiversity in different geographic clusters (e.g., ecoregions, biomes) within which organisms are assumed to have similar responses to environments. For example, regional factors have often been used to infer environmental drivers for different populations in niche modelling and biodiversity mappings (Jetz *et al.*, 2019). Whilst it is becoming widely recognised that species respond differently to environmental pressures and the relationship between them may vary at different scales (Jarzyna & Jetz, 2018; Tucker *et al.*, 2018; Owen *et al.*, 2019; Rapacciuolo *et al.*, 2019), macroecological studies like these continue to use predefined geographic clusters to carry out the analyses and recognise diversity patterns. This is likely owing to two reasons. First, it is a classic approach to observe and record biological progress at a local scale and summarise the larger-scale biological patterns in a bottom-up way, where an assumption of similarity due to geographic proximity is easily adopted. Second, although there has been extensive data collection for biodiversity surveys, it remains challenging to sample a whole given area at large scales to capture all its diversity changes, especially for long-term biological survey programmes that require substantial coordination and supports. Thus, regional diversity patterns are calculated from samples within them, and geographic structure is used *per se*.

However, using geographic structure to define and analyse patterns of diversity change may introduce biases for two reasons. First, the spatial distribution of diversity is highly

heterogeneous (Gaston, 2000), which means diversity in the same predefined geographic cluster can still be different. Second, given increasing human effects on nature, divergent diversity trends can also be observed in regions that are geographically close but experience human disturbance in various degrees. This suggests events that can change diversity trends may not match simple geographic structures. Therefore, patterns of diversity change that are recognised by different geographical clusters may not effectively capture temporal diversity patterns. However, although such biases may exist, analyses that have estimated diversity change have used geographic structure to delineate large-scale patterns of diversity change, such as ecoregions (Harrison *et al.*, 2018; Sano *et al.*, 2019), continents (Kerr *et al.*, 2015; Blowes *et al.*, 2019; Soroye *et al.*, 2020), bird conservation regions (Jarzyna & Jetz, 2018), country boundaries (Normander *et al.*, 2012), and little attention has been paid to whether patterns of diversity change can be effectively recognised by geographically clustering.

Here, we ask: should geographic structure be used as a default rule to recognise diversity patterns? To address this question, we propose a framework that tests whether times-series identified as having similar behaviour are geographically structured. We first recognise patterns of diversity change based on behaviours of diversity time-series neglecting their geographic locations. As such, diversity time-series with similar trends in the variability rather than geographically close to each other are recognised as having the same pattern. We then test the spatial dependence of time-series within the same pattern. Therefore, a geographic structure is found when diversity time-series that have a similar pattern on behaviours of temporal change tend to be geographically clustered

(Figure 1A-1D). Otherwise, the time-series are randomly distributed (Figure 1E-1F), signalling that geographical recognition of diversity patterns is likely biased. We illustrate this approach with North American Breeding Bird Survey data, which are collected annually over 5000 survey routes located across the continent of North America since 1966 (Pardieck *et al.*, 2020). To incorporate multiple facets of diversity, we calculate taxonomic, functional and phylogenetic diversity for all time-series. As a comparison, we complement this framework using analysis of a remote-sensing dataset (MOD13C2 MODIS/Terra Vegetation Indices) (Didan, 2015) in a vegetation index (EVI) in the contiguous United States under 100% and 0.1% coverages, respectively, which we expect *a priori* to demonstrate very strong spatial structuring.

2 MATERIALS AND METHODS

2.1 Non-geographic framework

2.2.1 Pattern recognition

Diversity change time-series are inherently likely to show serial autocorrelation (Daskalova *et al.*, 2021), and methods used to group diversity time-series should incorporate this. Here, we used self-organising maps (SOMs; Kohonen, 1997) to determine the patterns of different diversity time series. SOM is based on an artificial neural network and uses an unsupervised learning method, well adapted to complex data analyses. As an informative and intuitive method in feature extraction, SOM has found wide application in a variety of disciplines for clustering, classification, dimensionality reduction and data visualisation (Liu *et al.*, 2016). Some examples of the application of SOM in ecology are: determining representative species (Park *et al.*, 2006); estimating

FIGURES

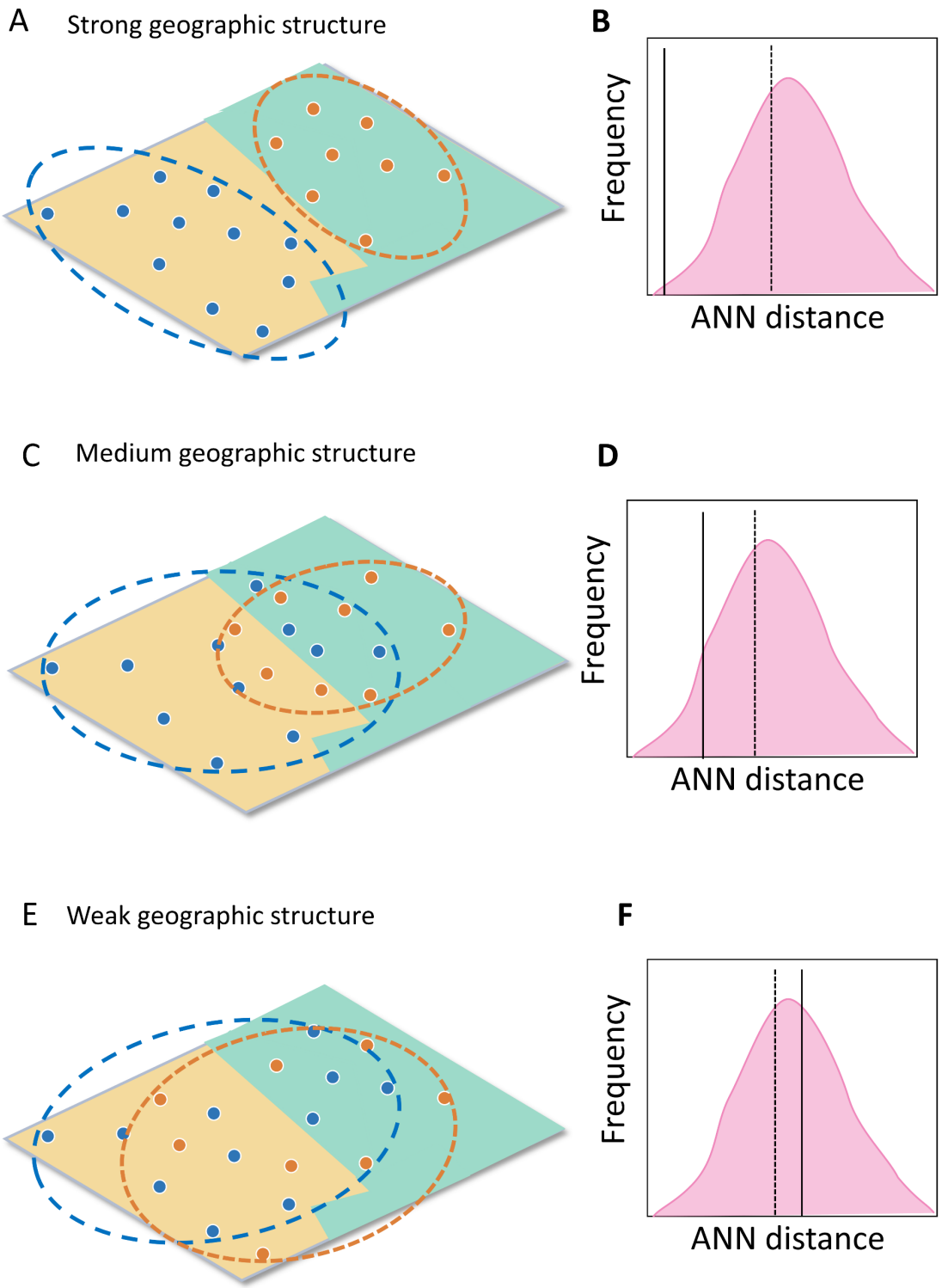
A Strong geographic structure
B
Frequency
ANN distance
C Medium geographic structure
D
Frequency
ANN distance
E Weak geographic structure
F
Frequency
ANN distance

Figure 1. Conceptual framework to test spatial dependence of time-series. A – B Strong geographic structures in recognised patterns of diversity change. **C – D** Medium geographic structures in recognised patterns of diversity change. **E – F** No evidence for geographic structures underlying the recognised patterns of diversity change. We recognise patterns of diversity change based on the behaviour change of different sample time-series. We calculate an average nearest neighbour (ANN) distance to measure geographic proximity of different locations. ANN distance from the real diversity time-series will fall to the left of the histogram of ANN distances of randomly generated locations supporting that geographic structure is important for pattern recognition **(B & D)**, while ANN distance from real diversity time-series adhering to the non-geographic pattern recognition will fall in the middle of the distribution **(F)**. Points in A, C, and E with the same colour surrounded by a dotted circle represent that they have similar diversity change and are recognised into the same pattern. Solid lines in B, D and F represent the ANN distance of the real diversity time-series, and dashed lines represent the average ANN distance for a set of random samples.

invasive species establishment (Gevrey *et al.*, 2006); investigating fish assemblages (Penczak *et al.*, 2012); modelling temporal evolution of Pacific surface chlorophyll (Huang *et al.*, 2017).

In an SOM algorithm, high-dimensional datasets are projected onto a lower-dimensional space (typically two dimensional), meanwhile preserving the similarity and the difference between the input data vectors. The process is organised by automatically detecting relevant subgroups of similar input vectors and generating neurons (virtual vectors) that describe the coordinates of centres of the subgroups. A neuron in a network responds to a given subgroup of similar input vectors and moves closer with the addition of new input vectors to it. Whilst a classic result from a SOM is a map (where the datasets to be classified are mapped into map nodes), the neurons that are neighbours on the map are expected to represent similar patterns; consequently, dissimilar patterns are expected to be distant from each other on the map. The training process iterates and tunes the network based on a preselected number of groups (hence, self-organising).

One of the most challenging steps in using SOM is to choose the number of groups. Topographic and quantisation errors (Kohonen, 2012) have been proposed to help determine the number of groups. The topographic error (TE) denotes the continuity of the mapping. Here, we calculated TE by the average distance between all pairs of most similar neurons of input vectors. TE, therefore can measure the topographic preservation and the accuracy of the mapping in topology.

$$\mathrm{TE} = \frac{1}{n}\left(\sum_{i=1}^{N} \min\|u_i - u\|\right),$$

where N is the number of neurons, and $\|u_i - u\|$ is the topographic distance between a given neuron and all other neurons.

The quantisation error (QE) represents the average distance between each input vector and its neuron.

$$\mathrm{QE} = (\sum_{i=1}^{N} \|x_i - u_c\|),$$

where N is the number of the input diversity time series, and $\|x_i - u_c\|$ is the topographic distance between every input vector and its neuron. Usually, small values of TE and QE suggest a good performance of the SOM model. However, QE and TE gradually decrease as the number of neurons increases and thus can only help determine the optimal number of neurons at a local scale (Park *et al.*, 2018).

SOM models can be applied directly to time-series data (Vesanto & Alhoniemi, 2000). We used the SOM model as a clustering and pattern recognition method to investigate temporal diversity patterns. Specifically, the input diversity time series are iterated by SOM to find the best matching neuron. Locations with similar diversity variability (i.e., diversity range and variation) will be taken as one group. Only once the data were classified on their temporal diversity variability were the geographic distribution of the time-series identified and plotted. We generated nine groups of diversity time-series and four groups of EVI time-series to explore their temporal change for the relatively smaller TE and QE of these numbers (Figure S1 & S2), which can also efficiently extract patterns of diversity and EVI variability. To contrast diversity variability with that from other numbers of groups, we also calculated the SOM models of 5×5, 5×4, 4×4 and 2×2

map size. We employed the 'supersom' function of the 'kohonen' package in R 4.0.1 (https://www.r-project.org). All SOM models were performed with a hexagonal structure and Gaussian neighbourhood function. Taxonomic, functional and phylogenetic diversity were used simultaneously with the same weight in each SOM model.

2.1.2 Spatial dependence

We used a Monte Carlo test with the average nearest neighbour (ANN) distance to test spatial dependence (Clark & Evans, 1954) in membership of the groups of time-series. $ANN = \frac{\sum_i^n d_i}{n}$, where d_i corresponds to the distance between feature i and its nearest neighbouring feature, and n is the number of features. The great circle distance on a WGS84 ellipsoid was used for all the distance calculations. Distance in raster data is calculated by the centres of each cell. For a given group of time-series that have the same pattern, we randomly selected an equal number of time-series to the number of time-series of that group from across all time-series analysed. Then the ANN distance for locations of the randomly selected time-series was calculated. We did not generate random points across the space for randomisation, because the biological surveys are often not randomly located (e.g., avoiding overlap). That process might be explicit (i.e. the people who organise the surveys specify this), or it might not be (e.g. it just results from the decisions that individuals make, but they make these in relation to other people's choices). The randomisation process was replicated 1000 times to generate a density histogram showing the distribution of ANN distances of the random time-series. A pseudo p-value was calculated to show the probability of incorrectness if rejecting the geographic independence hypothesis that diversity time-series that have the same pattern are

randomly distributed:

$$P = \frac{min(N_{greater} + 1, N + 1 - N_{greater})}{N + 1}$$

where $N_{greater}$ is the number of simulated ANN distances greater than the real ANN distance, and N is the number of replications. We did not remove locations that might lead to spatial pseudo-replications as here we aimed to test the geographic proximity of diversity time-series, which would be reflected by the results of the above analysis (e.g., p-value).

2.2 North American Breeding Bird Survey data

2.2.1 Example data

We used North American Breeding Bird Survey (BBS) data to investigate the biodiversity changes in different diversity facets (Pardieck *et al.*, 2020). BBS is a long-term avian monitoring program that tracks the population dynamics of breeding birds and follows a strict survey protocol allowing for yearly comparisons. BBS data are collected once per year in June over 5000 survey routes that are located across the continent of North America. Each survey route is approximately 40km long, with 50 stops, and split into five segments. At each stop, the birds will be detected when they are seen or heard within a 400m radius for 3 minutes. Generally, the trained observers record the stop ID, the presence and abundance of each species encountered. The sampling for each whole route is conducted over approximately five hours in the early morning.

BBS data from the early years of the survey are limited due to insufficient sample size and spatial coverage, so we excluded those from 1966 to 1972. To keep the integrity of

temporal coverage and obtain enough samples, for the period after 1972, we retained the routes with gaps of less than three years' duration and then conducted a multivariate imputation by chained equations (MICE; van Buuren & Groothuis-Oudshoorn, 2011), as implemented by the 'mice' package in R, to fill the gaps after diversity calculation. MICE has a better prediction quality and produces less biased estimates than other imputation methods in risk models using regression (Ambler *et al.*, 2007). We used a random forest algorithm (Breiman, 2001) for MICE, as it had high performance, required little computational time and was good at dealing with high dimensional data (Pantanowitz & Marwala, 2009; Penone *et al.*, 2014). We removed from all routes records for unidentified species and analysed a total of 911702 records (20721 per year) from 316 out of 5690 survey routes with less than three years' data gaps during 1973-2016. We imputed a sum of 331 data gaps from 214 routes based on all taxonomic, functional and phylogenetic records for each survey route.

2.2.2 Diversity measures

To compare taxonomic, functional and phylogenetic diversity in a consistent framework, we calculated these using an abundance-weighted measure, Rao's quadratic entropy (Rao, 1982):

$$\mathrm{Q} = \sum_{ij} d_{ij} p_j p_j$$

where d_{ij} is taxonomic, functional or phylogenetic diversity dissimilarity between each pair of species *i* and *j*, while $p_i$and $p_j$are their relative abundance. We then calculated the three diversity indices for a given time-series for every year.

For taxonomic diversity, the distance between all species is the same ($d_{ij} = 1$), and Rao's Q, in this case, is equivalent to the Gini-Simpson index, which usually measures the probability of interspecific encounter (Hurlbert, 1971). For the calculation of functional diversity, we used 4 categories of 16 traits from Elton Traits 1.0 (Wilman *et al.*, 2014). These traits, which are assumed to represent key Eltonian niche dimensions, comprised: body mass, diet (i.e., the proportional use of invertebrates, vertebrates, carrion, fresh fruits, nectar and pollen, seeds, and other plant materials in species' diet), foraging niche (i.e., prevalence of foraging below water surfaces, on water surface, on terrestrial ground level, in understory, in mid-canopy, in upper canopy, and aerial), and broad habitat types (i.e., pelagic or not). We gave equal weights to each trait category, which resulted in weights for body mass and broad habitat type of 1, and 1/7 for each diet and foraging niche variable. Functional distance was calculated using a multivariate trait dissimilarity of Gower's distance (Gower, 1971) for each pairwise species (Pavoine *et al.*, 2009), with functional diversity calculated as the subtree length on the UPGMA (Unweighted Pair Group Method with Arithmetic Mean) dendrograms of these distances. Phylogenetic distance was calculated using 100 phylogenies sampled from a full pseudo-posterior distribution of phylogenetic trees (http://birdtree.org). The mean phylogenetic diversity across these 100 dendrograms was calculated. All three diversity facets were standardised by $SD_i = (D_i - min(D))/(max(D) - min(D))$ before further analysis, where SD_i is the standardised diversity, D is the diversity and $D = (D_1, \dots, D_n)$.

2.2.3 Relationship between different diversity facets

To investigate the correlation of functional-taxonomic, phylogenetic-taxonomic and functional-phylogenetic diversity in each group of diversity time-series, we adopted generalised additive models (GAM) and included the year of a given time-series as a random effect. We calculated the deviation explained and 95% confident interval for all the groups to measure the correlation of different pairs of diversity facets.

2.3 MODIS/Terra Vegetation Indices

We used enhanced vegetation index (EVI) from a remote sensing product (MOD13C2) (Didan, 2015) as a test of the framework in different sample coverages for a system where we expect strong spatial clustering. The EVI provided biomass information and can be used to quantify the vegetation greenness. The product provided a monthly EVI in a 5,600-m resolution from 2000 – 2021 across the globe. As we aim to test the spatial dependence of EVI time-series, we here quantified their annual change in September when the activity of vegetation is usually at a maximum and relatively constant over the year (Villamuelas *et al.*, 2016) in the contiguous United States to simplify the calculation. We first applied our framework with full spatial coverage of the study area (326782 time-series) and then a partial coverage by randomly subsampling the EVI time-series for a 0.1% sample coverage (326 time-series).

3 RESULTS

To test the relative fit of geographic structuring, we assessed the spatial dependence of time-series within each pattern recognised by changes in their variabilities using two

datasets with different spatial sample coverages. We found no evidence of stronger geographic structure on diversity change of North American breeding birds than random. We found that the average distance between the survey routes lay in the middle part of the distance frequency curve calculated from randomly distributed points, although the number of survey routes within eight of the nine groups varied (Figure 2). Similar results were also found for other numbers of groups of diversity time-series (Figure S3-S6).

The temporal trends, range and correlation of taxonomic, functional and phylogenetic diversity varied across the different groups of diversity time-series (Figure 3 & Figure S7-S10). Taxonomic diversity showed a gradual increase in four patterns (Figure 3-1, 3-4, 3-7 and 3-9) and decline or no change in the other groups (Figure 3-2, 3-3, 3-5, 3-6 and 3-8). Functional and taxonomic diversity were positively correlated in most groups (DE = $0.44, 95\%\ CI = 0.30{\sim}0.59$; Figure S11). Functional diversity showed similar trends to taxonomic diversity, but the change rates were different.

The correlation between taxonomic and phylogenetic diversity varied less in groups of diversity time-series (Figure S3). Phylogenetic diversity had a trend of slowly increasing or staying flat as taxonomic diversity increased (DE = $0.16, 95\%\ CI = 0.09{\sim}0.23$). The correlation between functional and phylogenetic diversity differed more in groups of diversity time-series compared to the correlation between taxonomic and functional diversity, or taxonomic and phylogenetic diversity (DE = $0.41, 95\%\ CI = 0.32{\sim}0.52$). In most of the groups (seven out of nine groups), functional diversity increased faster than the increase of phylogenetic diversity and could also increase more slowly or even decline

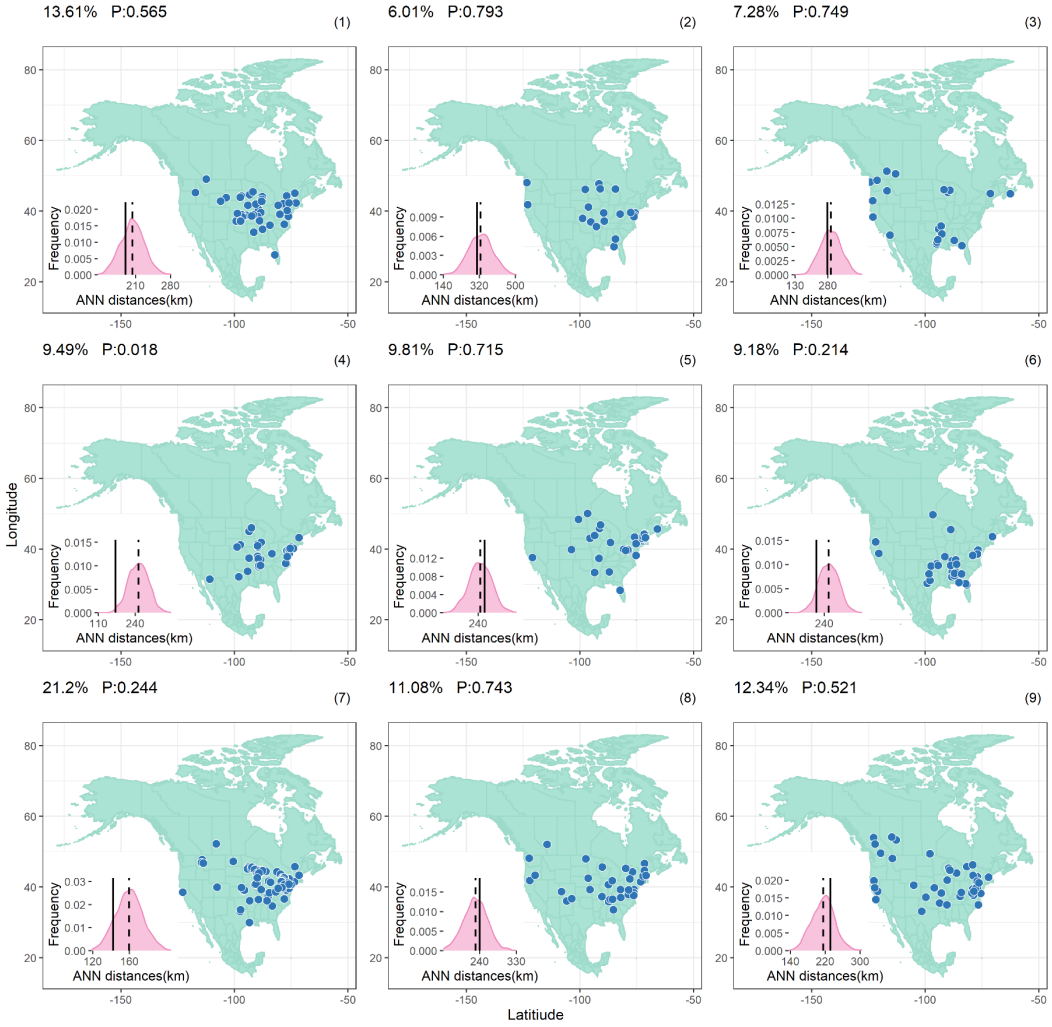

Figure 2. Distribution of survey routes in North American Breeding Bird Survey and spatial independence test. Each panel presents the distribution of diversity time-series that have the same pattern as identified by the SOM. The inset density plot shows the distribution of the ANN distance of 1000 Monte Carlo tests. Solid lines in the density plot represent the average nearest neighbour (ANN) distance of the survey routes, and dashed lines represent the mean value of ANN for 1000 random samples. Blue points represent start locations of each survey route. Percentages on the left top of each panel denote the percentage of time-series in that group to all time-series. Pseudo p-values represent the probability of incorrectness if rejecting the geographic independence hypothesis that diversity time-series that have the same pattern are randomly distributed.

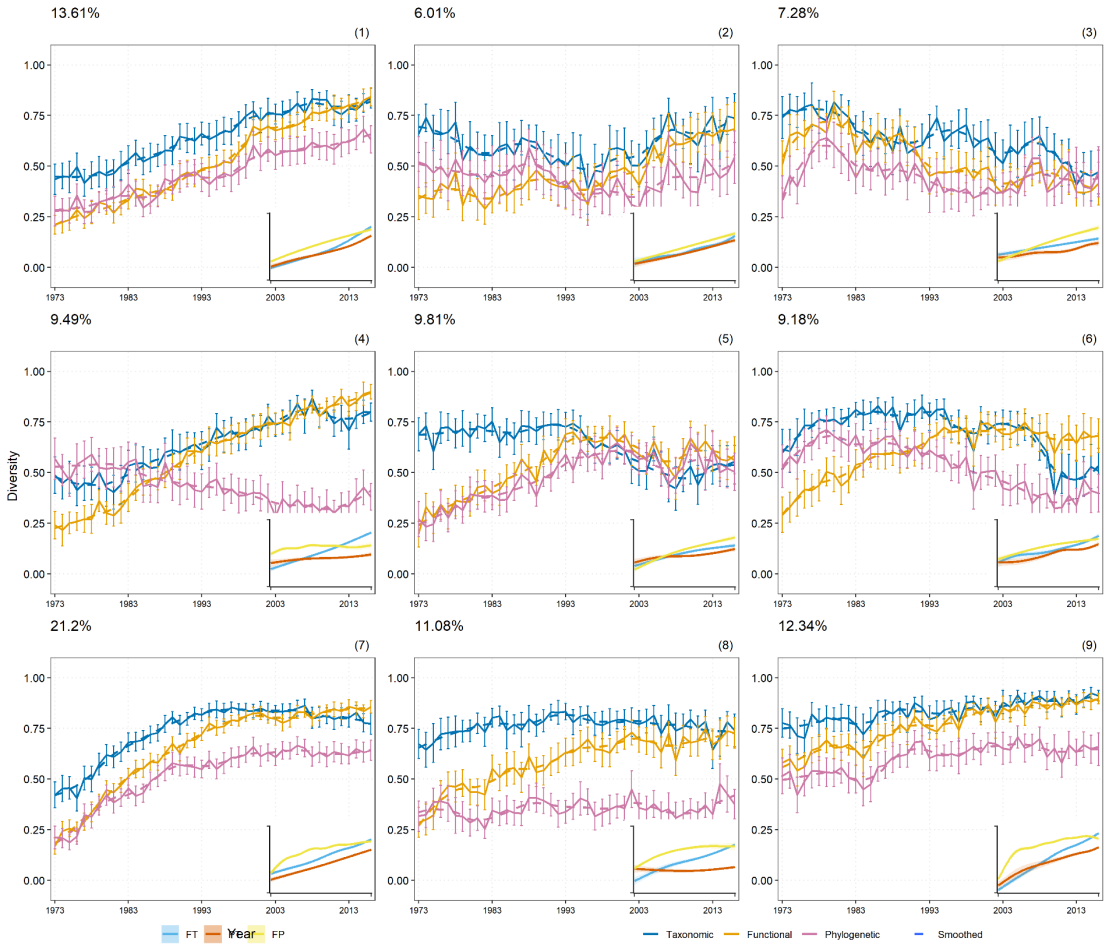

Figure 3. Temporal changes of taxonomic diversity, functional and phylogenetic diversity in North American Breeding Birds. Each panel denotes the change of diversity time-series that have the same pattern. Error bars represent a 95% confidence interval. Nonlinear regressions (a loess sliding window with a 33% range width; smoothed line) of the diversity facets were added to describe the major temporal trajectory at each group. Inner plots represent the correlation between diversity facets. FP is how functional diversity changes with phylogenetic diversity, FT is how functional diversity changes with taxonomic diversity, and PT is how phylogenetic diversity changes with taxonomic diversity.

with the rise of phylogenetic diversity (Figure 3).

We found EVI time-series that were recognised to have the same pattern of temporal change have a clear geographic structure under both full and 0.1% sample coverages (Figure 4). We found strong evidence that distribution of the time-series is distinct from random across all groups (Figure S12-S17). Hence, this method is able to detect and return strongly spatially clustered signals.

4 DISCUSSION

Despite the frequent use of geographic structure in studies of the distribution of biodiversity (Gaston, 2000; Willig *et al.*, 2003; Devictor *et al.*, 2010; Blowes *et al.*, 2019), we reveal that using geographic structure as a default rule to recognise diversity patterns may be biased; there are other kinds of structure in such data that are important to understand diversity patterns.

We proposed a non-geographic framework to group biodiversity time-series based on a pattern recognition method (i.e., SOM) and highlight potential geographic biases to understand patterns of diversity change. Specifically, we classified the time series that varied similarly in the temporal trend as having the same pattern and tested whether the geographic distribution of routes of the same pattern is random. Using North American Breeding Bird Survey data, we demonstrated that diversity time-series that have the same pattern of temporal change could be independent of their geographic locations. This implies that in large-scale studies, geographic proximity may not correspond to shared

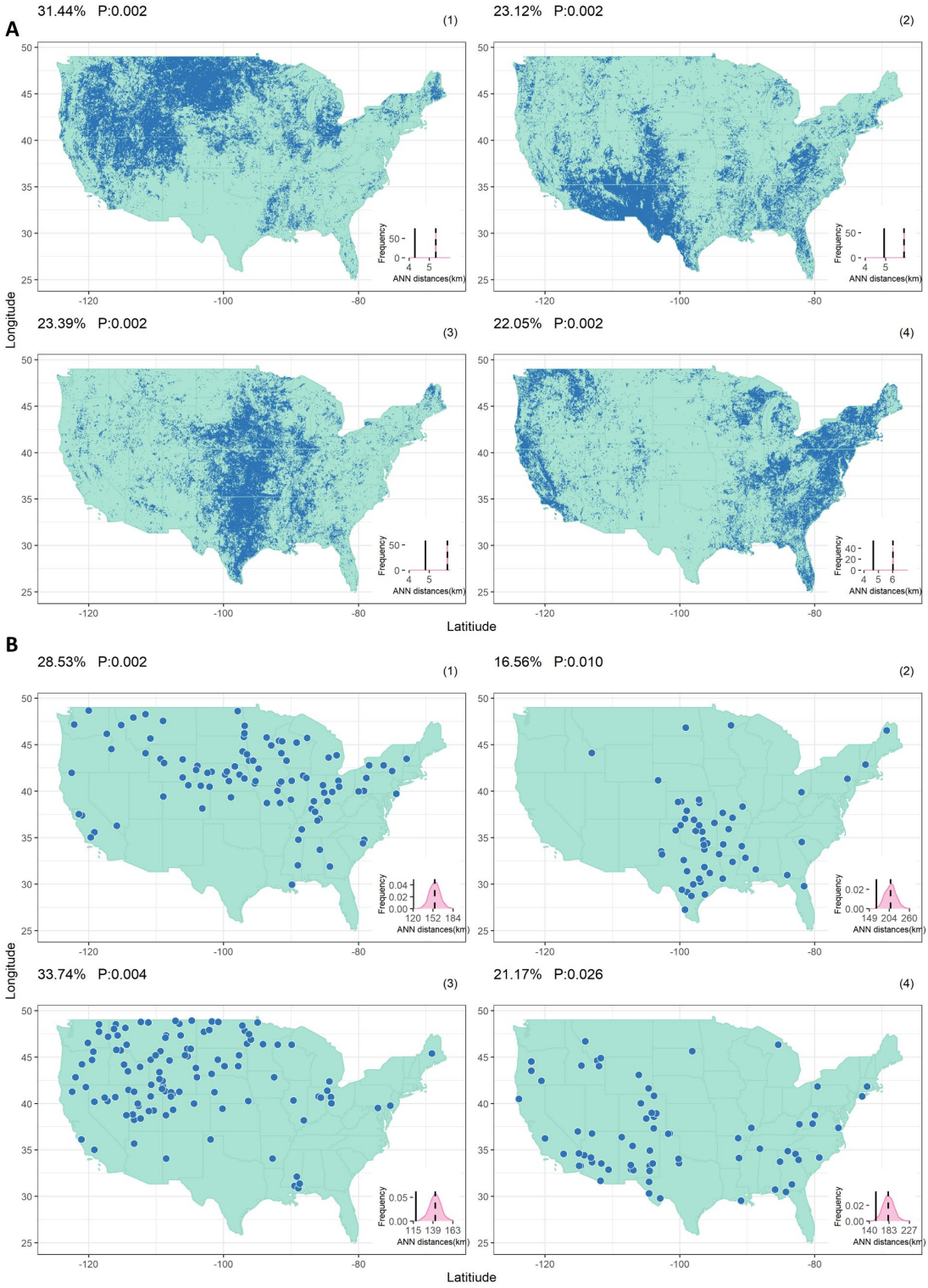
A
31.44% P:0.002
(1)
23.12% P:0.002
(2)
23.39% P:0.002
(3)
22.05% P:0.002
(4)
Longitude
Latitiude
Frequency
ANN distances(km)
B
28.53% P:0.002
(1)
16.56% P:0.010
(2)
33.74% P:0.004
(3)
21.17% P:0.026
(4)
Longitude
Latitiude
Frequency
ANN distances(km)

Figure 4. Distribution and spatial independence test of enhanced vegetation index (EVI) time-series in the contiguous United States under full (A) and 0.1% (B) spatial sample coverages. Each panel presents the distribution of EVI time-series (blue pixels) that have the same pattern. The inset density plot shows the distribution of the ANN distance of 1000 Monte Carlo tests. Solid lines in the density plot represent the average nearest neighbour (ANN) distance of the locations of EVI time-series, and dashed lines represent the mean value of ANN for 1000 random samples. Percentages on the left top of each panel denote the percentages of time-series in that group to all time-series. Pseudo p-values represent the probability of incorrectness if rejecting the geographic independence hypothesis that EVI time-series that have the same pattern are randomly distributed.

temporal diversity trends. Ignoring the possible variation between time-series of a given geographic cluster, e.g., simply taking all time-series as a whole, could bias the understanding of biodiversity change.

By identifying geographically disparate patterns of similar diversity change, we emphasise the complex resultant structure of biodiversity (Gaston, 2000; Brooks *et al.*, 2006) from two perspectives. First, from a spatial perspective, biodiversity is usually understood as having multiple facets, including taxonomic and species composition, ecosystem function and service potential, evolutionary history, etc., which leads to the complexity in its distribution and structure (Tilman, 1982; Gaston, 2000; Grenyer *et al.*, 2006; Petchey & Gaston, 2006). Communities in neighbouring regions may face different environmental and human pressures, and as a result, have divergent trends in diversity change. Therefore, estimation of large-scale diversity patterns may be biased by using geographic structure *a priori* and not distinguishing the behaviours between diversity time-series. Second, in temporal contexts, biodiversity change is also influenced in complex ways such as the exploitation of biological resources, the introduction of exotic species, climate and land-use change (Sax & Gaines, 2003; Mantyka-Pringle *et al.*, 2012; Newbold *et al.*, 2015), which in turn may influence the behaviours of surveyors and estimation of diversity trends (Zhang *et al.*, 2021). This is particularly important for recognising patterns of diversity changes considering that spatial sample coverage of even the most extensive biodiversity datasets is believed to be less than 7% of the Earth's surface at a 5-km resolution (Hughes *et al.*, 2021), and analyses estimating long-term diversity trends may abandon short time-series or time-series with data gaps (Zhang *et*

al., 2021). Using geographic structure *a priori* to seek patterns of diversity change can result in failures to incorporate diversity changes that were not recorded and bias diversity estimation. Given the difficulties to improve the spatial coverage of long-term biodiversity surveys, the non-geographic framework that organises diversity time-series independently of their relative or specific locations also provides a novel way to recognise large-scale diversity patterns for existing diversity time-series datasets.

As for patterns of North American Breeding bird diversity, we found functional and phylogenetic diversity changed disproportionately to taxonomic diversity in multiple groups. Specifically, significant changes in functional diversity were accompanied by more minor changes in taxonomic diversity. The correlation between taxonomic and functional diversity was strong and positive in the long term, which was a likely consequence of the replacement of functionally redundant species with unique ones. Furthermore, changes of phylogenetic diversity in the groups were smaller than or even opposite to what would have been expected given the concomitant changes in taxonomic and functional diversity. Correspondingly, phylogenetic diversity showed a tendency to level off and even decline with increasing taxonomic and functional diversity. This phylogenetic homogenisation implies that the bird assemblages have perhaps undergone recruitment of, or even replacement by, closer relatives of species already present. The fast adaptive radiation of colonising species could also contribute to the high levels of taxonomic and functional diversity and low levels of phylogenetic diversity across North America (Jarzyna & Jetz, 2017).

We also tested our framework with an EVI time-series dataset. The results showed strong evidence that EVI time-series of the same pattern are geographically structured under both full and 0.1% spatial sample coverage. This suggests that geographic structure may work well in understanding ecological changes in plant biomass (Holt *et al.*, 2013; Smith *et al.*, 2018) but may not play a meaningful role in delimiting more complex patterns of animal diversity change. Therefore, the results emphasise the geographic biases in recognising patterns of diversity change and the importance of our framework to partition biodiversity change by the similarity of time series.

Since we focus on the geographic bias in long-term diversity estimations with existing diversity time-series data, there may be temporal or spatial scale-dependent effects on this bias. Future work could explore interplays between different spatial sample coverages and lengths of diversity time-series and how they may influence the geographic bias. Future work could also concentrate on identifying drivers of the non-geographic biodiversity patterns extracted from time series, which can be achieved by determining (non-)geographic patterns in the temporal variation of biotic and/or abiotic factors and exploring their potential mismatch with recognised diversity patterns. Then by analysing the degree of mismatch between diversity and factor patterns, it could be possible to establish networks of ecological interactions and their contributions to the dynamic of diversity change in each pattern. In doing so, recognising non-geographic patterns also provides a bridge between empirical systems and theoretical interaction frameworks, such that has been used in identifying the relationship between patterns of phytoplankton and eddy lifecycles in oceanography (Huang *et al.*, 2017).

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AUTHORS' CONTRIBUTIONS

WZ conceived the ideas and all authors contributed to the methodology design; WZ analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

BBS data used for these analyses are online https://www.pwrc.usgs.gov/bbs/, and EVI datasets are available on https://lpdaac.usgs.gov/products/mod13c2v006/

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4

Habitat change biases diversity sampling and estimation

Report

Habitat change and biased sampling influence estimation of diversity trends

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SUMMARY

Recent studies have drawn contrasting conclusions about the extent to which local-scale measures of biodiversity are declining and whether such patterns conflict with the global-scale declines that have attracted much attention.[1] A key source of high-quality data for such analyses comes from longitudinal biodiversity studies, which sample a given taxon repeatedly over time at a specific location.[2] There has been relatively little consideration of how habitat change might lead to biases in the sampling and continuity of biodiversity time series data, and the consequent potential for bias in the biodiversity trends that result. Here, based on analysis of standardized routes from the North American Breeding Bird Survey (3,014 routes sampled over 18 years),[3] we demonstrate that major local habitat change is associated with an increase in the rate of survey cessations. We further show that routes that were continued despite major habitat changes show reduced diversity. By simulating potential rates of loss, we show that the underlying real trends in taxonomic, functional, and phylogenetic diversity can even reverse in sign if more than a quarter of diversity is lost from routes that ceased and are thus no longer included in surveys. Our analyses imply that biodiversity loss can be underestimated by biases introduced if continued sampling in longitudinal studies is influenced by local change. We argue that researchers and conservation practitioners should be aware of the potential for bias in such data and seek to use more robust methods to evaluate biodiversity trends and make conservation decisions.

RESULTS AND DISCUSSION

Longitudinal studies play a crucial role in understanding how biodiversity is changing in response to direct and time-lagged processes. Most studies evaluating temporal diversity trends are based on consecutive time series records or at least records including the beginning and the end of the objective study periods. Often, the data gaps in time series datasets or subsets with relatively large data gaps are ignored or imputed with simple methods.[4–6] If such gaps in time series are from sites disproportionately affected by biodiversity and richness declines, they may bias the long-term datasets toward relatively undisturbed communities and underestimation of biodiversity responses to human pressure. One mechanism by which this might occur in long-term biological monitoring programs is if the habitats in or surrounding the survey sites experience abrupt modification.[7] If the sampling of such sites ceases disproportionately as a result, locations showing the greatest biodiversity loss would tend not to be incorporated in a final dataset.

To determine the potential for impacts of major habitat change on estimating biodiversity trends, here, we evaluated the association between major habitat change and cessation of sample routes of a long-term biological monitoring program, the North American Breeding Bird Survey (BBS).[3] BBS data are collected once per year by more than 2,500 trained recorders in June over 5,000 survey routes that are located randomly within physiographic strata across the continent to sample habitats that are representative of the entire continent. They have frequently been used for estimating regional-level bird population trends and prioritizing species and areas for conservation action.[2,8–10] We estimated yearly habitat change using a land cover product from the Terra and Aqua combined Moderate Resolution Imaging Spectroradiometer (MODIS), Land Cover Climate Modeling Grid (CMG) Version 6 (MCD12C1)[11] from 2001 to 2018 at 0.05° resolution. We then calculated the habitat change for each route as the difference between the focal year and the preceding year in the proportion of 16 habitat types around the 3,014 neighborhoods of the routes. We used multiple non-overlapping ranges to characterize the major habitat change (i.e., whether the total change of 16 habitat types is $\geq$5% and <10%, $\geq$10% and <15%, $\geq$15% and <20%, $\geq$20% and <25%, $\geq$25% and <30%, and $\geq$30% of the total buffer area). For example, we would define a change from 13% wetland to 6% farmland and 7% grassland of the total neighborhood around a route as a 10%–15% change. In cases where habitat did change, we defined two cases: survey ceased (habitat change) routes were

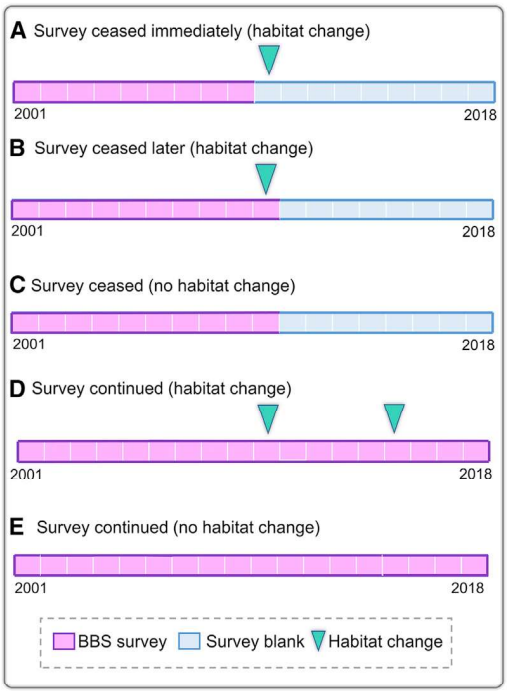


Figure 1. Schematic illustration of potential sequences of survey cessation and habitat change

(A) The survey cessation occurs 1 year in advance or in the same year as the major habitat change.

(B) A 1-year-delayed survey cessation after the major habitat change.

(C) The survey ceased without being associated with habitat change.

(D) The survey continued despite habitat change.

(E) Survey continued without any habitat change. Note: survey data might contain random missing years, but only those surveys that ceased and did not resume by the end of the study period are defined as ceased surveys in this study.

those where a survey stopped and did not restart by the end of the study period (i.e., 2018); otherwise, they were defined as survey continued (habitat change) routes (see Figure 1 for illustration). Where necessary, we calculated null randomization distributions by reallocating the observed habitat changes randomly across all routes.

To understand how habitat loss affects diversity, we used three diversity indices calculated from the BBS data: taxonomic diversity (species richness); functional diversity as the proportion of a hyperspace defined on Elton Traits; and phylogenetic diversity via the shared root of the bird phylogeny (for full details, see STAR Methods). We calculated diversity trends in all three metrics across time in two ways: the annual change between 2001 and 2018 by fitting regression models to time and a comparison of 3-year periods at the beginning and end of the dataset (i.e., 2001–03 and 2016–18, to avoid the potential effect of unusual or abnormal years) as the difference of diversity between the 2016–18 and 2001–03 periods divided by diversity of the 2001–03 period. For both approaches, we estimated effects of habitat change on biodiversity by comparing the diversity trend in survey continued (habitat change) routes and survey continued (no habitat change) routes. To assess the potential effect of no longer including those sites at which surveys ceased (and for which overall biodiversity change is, by definition, unknown), we simulated a range of values (from 0% to 100%) of diversity loss for the single year when a survey cessation happened, with diversity change at the average rate of survey continued routes afterward; while 100% diversity loss is an unlikely extreme scenario for this dataset, it might occur for habitat specialist taxa, and we included the full range to enable generality in our conclusions. We also simulated how overall diversity trends could be influenced across different proportions of survey ceased (habitat change) routes. In so doing, we asked how the continued incorporation of these sites would have influenced the rate of change in biodiversity in the overall sample.

Habitat-change-associated route cessation was a frequent, but not predominant, phenomenon in the BBS dataset: most routes that ceased did not have associated habitat change, and most habitat change was not associated with route cessation. However, we found that the minority of routes that did experience habitat-change-associated cessation would be sufficient to induce significant quantitative and qualitative changes in the interpretation of overall biodiversity trends.

We found that cases of a $\geq$5% major habitat change associated with a survey cessation occurred in 253 out of the total 3,014 BBS routes. Within the subset of 253 survey ceased (habitat change) routes, in 182 routes (72%), the survey cessation occurred 1 year before, or was contemporaneous with, the major habitat change (Figure 1A), while in the remaining 71 routes, the survey cessation occurred 1 year after the major habitat change (Figure 1B). Survey cessation that was not associated with our measure of habitat change was found in 920 BBS routes. We also found $\geq$5% major habitat change occurred in 1,535 BBS routes (52%) but was unrelated to any survey cessations; no major habitat change was detected in 1,226 BBS routes (41%).

Despite being low in absolute terms, we found the cessation of survey routes to be significantly associated with local habitat change. In many cases, the frequency of survey cessation (habitat change) is approximately double what would be expected if major episodes of local habitat loss are randomized across time and space (Figure 2). Despite being significantly associated with cessation, the relationship between the amount of habitat change and route cessation is complex. As the percentage thresholds of habitat change increase, survey cessation (habitat change) rates for both BBS and the random model decline, which suggests a relatively high proportion of habitat change is less likely to be related to a survey cessation than a habitat change of low proportion (Figures 2 and S1). Although sample sizes for the higher proportions of habitat change are small and higher percentage thresholds of habitat change within a year are experienced less frequently, the overall rate of survey cessation (habitat change) decreased as the severity of habitat change increased: 14% of routes experiencing a year with habitat change $\geq$5% and <10% also experienced a cessation of recording, with only 2.5% of routes experiencing $\geq$30% habitat loss undergoing cessation (Figure 2, 1 and 16). This may be due to the use of a relatively large study neighborhood for each survey route (Figure S2, approximately 300 km^2), so that even a small proportion of habitat change may represent a major habitat change along the survey route. For example, most habitat changes constitute less than 15% of the total

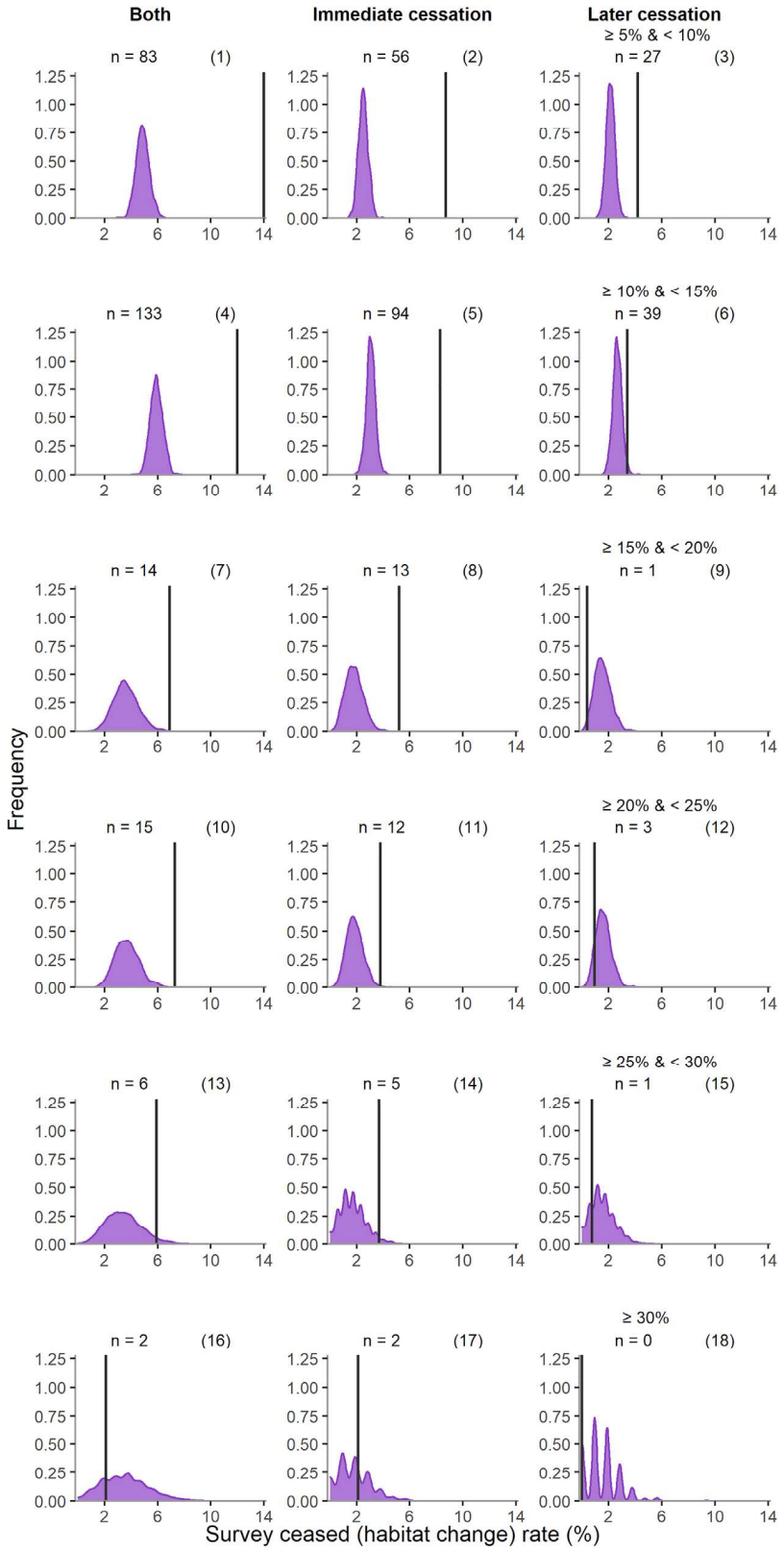
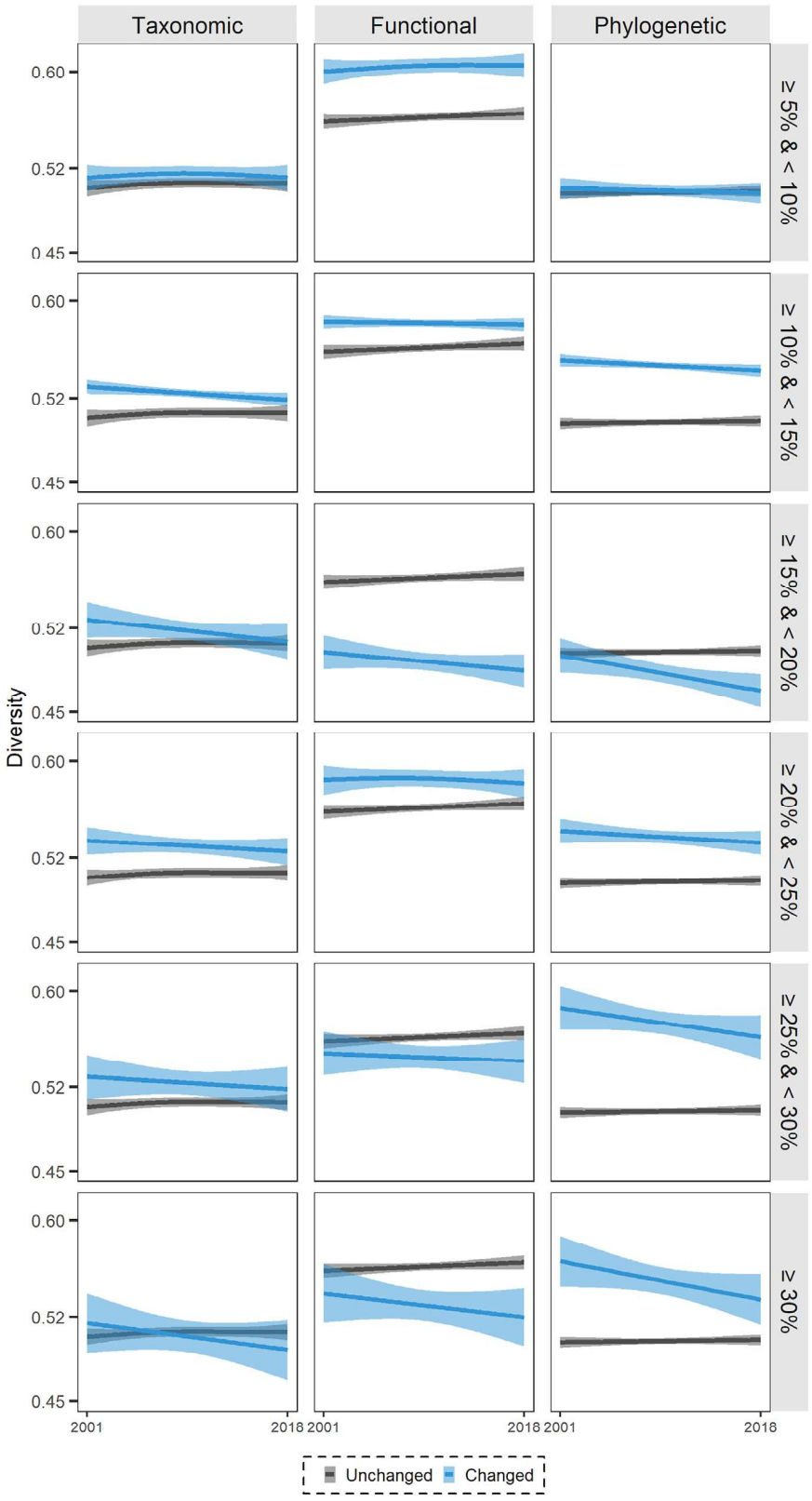


Figure 2. Frequency distribution of habitat change on survey routes

Density distribution of survey ceased (habitat change) rate for randomized habitat change (purple density plot) and the real habitat change (solid line) across different habitat change proportions and different cases. The survey ceased (habitat change) rate is calculated as the percentage of the number of survey ceased (habitat change) routes to total number of routes with habitat change. Numbers above each panel denote the number of survey ceased (habitat change) routes, and percentages on the right-hand side denote the habitat change categories. See Figure S2 for route distribution and summary.



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neighborhood (Figure S2), and 15% increase of a habitat type would result in the change of about 45 km^2 of the surrounding habitats. At the same time, the BBS survey was conducted based on routes randomly located across the continent, while landscape transformation to anthropogenic habitats (e.g., road expansion and commercial and residential development) by definition occurs in relatively pristine areas; this may lead to critical effects on a survey but usually does not account for a large proportion of the whole area (Figure S4) at this scale.[12] However, due to the relatively small sample size at more than 25% habitat change, how larger habitat change influences survey continuity needs more exploration.

We compared the trends of taxonomic diversity (TD), functional diversity (FD), and phylogenetic diversity (PD) for BBS routes with and without habitat change (Figures 3 and S3). In routes with no habitat loss, diversity metrics mostly increased over the sample period. This is likely caused by the rapid increase in biotic homogenization at these less disturbed areas, which may lead to a global loss of species but no change or even an increase in local-scale diversity.[6,13] However, diversity mostly decreased in routes with habitat change (Figure 3). The general result agrees with global-scale analysis by Jung et al.,[7] who demonstrated from analysis of species occurrence and land cover data that abrupt habitat change was associated with local taxonomic diversity loss. That surveys tended to cease under the conditions that were associated with reductions in biodiversity suggests that the estimation of biodiversity change using longitudinal biological monitoring data may be incomplete and biased if it ignores the potential for non-random sampling.

Estimation of the size of this effect is not straightforward. Biodiversity change in survey cessation (habitat change) and survey continued (habitat change) routes might be very different, and simply inferring change in the former by the pattern of change documented in the latter may be misleading. Here, we estimated the overall biodiversity trends had those routes where data collection stopped being included. We simulated diversity changes in survey ceased (habitat change) routes as different percentages of each route's diversity before cessation (Figure 4). Diversity in the subset of routes excluding survey ceased (habitat change) routes increased continuously to the mid-2000s, followed by a decrease (Figures 4B–4D), which is in accord with previous investigation of the temporal trends of North American bird diversity.[4] If survey ceased (habitat change) routes had been included, the overall diversity trend can be inverted from the observed growth to a decline depending on the extent of diversity loss in such routes. Specifically, the trend calculated by comparing diversity between the extreme 2001 and 2018 periods reversed if we assumed a quarter of diversity was lost in survey ceased (habitat change) routes, which account for 11% of the sampled routes in our study (Figure 4A). The assumed diversity loss for an inverted trend decreased as the proportion of ceased (habitat change) routes increased, while a more negative diversity trend was found if there was diversity loss in survey ceased (habitat change) routes and their proportion increased (Figure 4A). Our results indicate that biases in the collection of longitudinal data induced by non-random changes in sampling have the potential to significantly influence the estimation of overall biodiversity trends and highlight the magnitude of error that may be introduced when ignoring cessation bias.

Studies suggesting an absence of ubiquitous local species richness declines have been criticized for lack of baselines or reference conditions, variation in observers and their abilities, and for not using sufficiently long time series to achieve reliable conclusions,[14–17] although some analyses have suggested these potential weaknesses did not influence the conclusion that there has been no decline.[6,18] In this study, we draw attention to a different problem: the potential that non-random data gaps in biological monitoring programs, which might be caused by habitat change, may induce bias in estimating diversity trends. To exclude the effects of large data gaps, we only accounted for survey cessations that did not resume by the end of the study period, whereas a survey route that experienced a habitat-change-induced stop may also later restart. This might be the case if habitat transformation occurs between natural habitats or if a decision is made to sample secondary or successional habitats after disturbance. The overall rate of survey cessation (habitat change) may therefore be higher than we estimated here. Further studies quantifying biodiversity trends and the impacts of habitat change globally could benefit from distinguishing survey cessation with habitat change and survey cessation caused by other factors. A further issue, which we have not addressed here, is the possibility for positive reinforcement to create an additional bias. For example, if volunteers collecting survey data are more likely to persist in longitudinal surveys when local diversity trends are positive, this may lead to a further bias in longitudinal data, which would further mask larger scale trends. The interaction between biodiversity and the behavior of those collecting data on biodiversity is an under-studied area, worth further research.

Effects of changes of different habitat types on biodiversity are different.[19] Here, we focused on the change of the composition of different habitat types and did not differentiate between natural habitat losses and gains. We found no obvious trend for a certain habitat change type to be associated with survey cessation at less than 20% habitat change, while habitat change types that have higher probability to induce survey cessations at more than 20% habitat change are all between natural habitats or natural habitat mixed with croplands (Figure S4). This indicates that both gains and losses in natural habitat could cause survey cessations with no obvious difference at lower habitat change rates. Change between natural habitats could also induce survey cessations, e.g., the replacement of woodland by grassland could be regarded by a surveyor as no longer constituting a useful comparative time series. Although both changes of natural and

Figure 3. Temporal changes of taxonomic, functional, and phylogenetic diversity in survey continued routes

Nonlinear regressions (a loess sliding window with a 33% range width; solid line) of different diversity facets were used to describe the major temporal trajectories across multiple habitat change categories. All diversity values were scaled from 0 to 1. Color bands denote 95% confidence intervals. Number within the brackets is the sample size of that category. See Figure S3 for diversity comparisons between the beginning and the end of study period and also Figure S4 for summary on proportions of habitat change types.

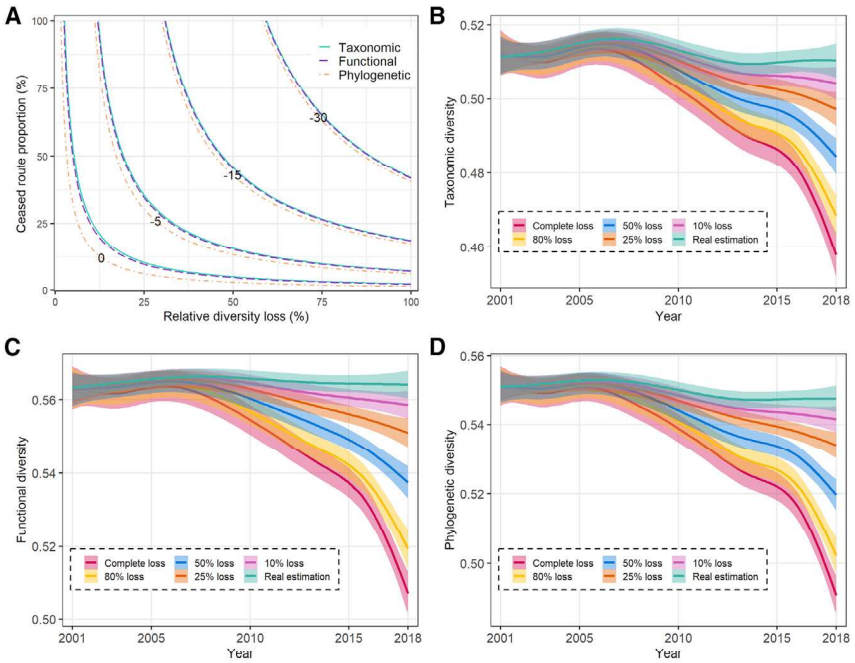

Figure 4. Temporal changes of taxonomic, functional, and phylogenetic diversity under assumptions that diversity in survey ceased (habitat change) routes reduced to different percentages of their diversity before cessation

(A) The effects of survey ceased (habitat change) route proportion and their relative diversity loss on estimation of diversity trends. Relative diversity changes were compared between 2001–2003 and 2016–2018 periods, assuming different percentages of diversity loss in survey ceased (habitat change) routes and different percentages of surveys ceased (habitat change routes) from the total numbers sampled.

(B–D) Temporal trends in three facets of biodiversity from 2001 to 2018. All diversity values were scaled from 0 to 1. The solid lines represent the smoothed spline (a loess sliding window with a 33% range width) with different colors indicating diversity loss in survey ceased (habitat change) routes of different percentages and color bands denoting 95% confidence intervals.

anthropogenic habitats could cause a reduction in biodiversity[7] and survey cessations, diversity after different types of habitat change and their impacts on the estimation of biodiversity trend might be different. We propose further studies distinguishing the impacts of natural and anthropogenic habitat changes and exploring whether different drivers of habitat change, such as agricultural conversion, urban expansion, or natural fires, have different impacts on the biodiversity trend estimation.

Evaluating biodiversity trends is of great importance.[1] Considerable debate on the generality of biodiversity trends across the globe has recently arisen due to divergent conclusions derived from two distinct approaches to estimating those trends.[1,20] One is spatial comparisons by which measures of diversity in sites that are disturbed by human activities are compared to those in undisturbed reference sites. Such spatial comparisons often show global biodiversity is declining.[21,22] The other is analysis of time series data that have been collated from studies using repeated measurements of biodiversity at individual locations around the planet, which sometimes show global biodiversity is not declining.[6,13,23] Because the time series datasets are distributed across different locations and over multiple geographic structures, the proliferation of such datasets and sometimes unexpected results have received considerable attention. Here, based on time series data of a long-term biological monitoring program, we show that the continuity of a biodiversity survey is more likely to be interrupted when major habitat changes occur and that the major habitat change often leads to the reduction of biodiversity. Therefore, potential bias exists in the estimation of biodiversity using time series data; the likely effect is that biodiversity loss is underestimated. We suggest researchers and conservation practitioners be aware of the potential bias and call for strategies, tools, and frameworks to continue to monitor the biodiversity change of major habitat change in the future.

STAR★METHODS

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SUPPLEMENTAL INFORMATION

Supplemental information can be found online at https://doi.org/10.1016/j.cub.2021.05.066.

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AUTHOR CONTRIBUTIONS

W.Z. and K.J.G. conceived the ideas, and all authors contributed critically to the methodology design. W.Z. performed the analyses and led the writing of the manuscript. All authors contributed to drafts of the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited data		
North American Breeding Bird Survey Data	U.S. Geological Survey's Patuxent Wildlife Research Center and Environment Canada's Canadian Wildlife Service	https://www.pwrc.usgs.gov/bbs/
Terra and Aqua combined Moderate Resolution Imaging Spectroradiometer (MODIS), Land Cover Climate Modeling Grid (CMG) Version 6 (MCD12C1)	NASA EOSDIS Land Processes DAAC	https://lpdaac.usgs.gov/products/mcd12c1v006/
Software and algorithms		
R	R Core team	https://www.r-project.org/
sp package	Pebesma and Bivand[24]	https://cran.r-project.org/web/packages/sp/index.html
rgdal package	Bivand et al.[25]	https://cran.r-project.org/web/packages/rgdal/index.html

RESOURCE AVAILABILITY

Lead contact

Further information for resources should be directed and will be fulfilled by the Lead Contact, Wenyuan Zhang (wenyuan.zhang@zoo.ox.ac.uk).

Materials availability

This study did not generate new unique reagents.

Data and code availability

This paper analyses existing, publicly available data. These accession numbers for the datasets are listed in the Key resources table. R code for performing our analyses is available at GitHub (https://github.com/plmyann/biotrends). Any additional information required to reanalyse the data reported in this paper is available from the lead contact upon request.

EXPERIMENTAL MODEL AND SUBJECT DETAILS

We used the North American Breeding Bird Survey data (BBS) to explore the effects of habitat change on the surveys of biological monitoring programmes, and subsequent estimation of biodiversity trends. The BBS is a long-term avian monitoring program which tracks the population dynamics of breeding birds and follows a strict survey protocol.[3] BBS data are collected once per year in June over 5000 survey routes that are located across North America. Each survey route is approximately 40km long. Routes are divided into 5 segments, each of ten stops at evenly spaced 800 m intervals, giving 50 stops for each survey route. At each stop, trained observers record the birds that are seen or heard within a 400 m radius in 3 minutes. No new data was collected for this study and no physical experiments were conducted.

METHOD DETAILS

Habitat Change Measure

We used a land cover product from the Terra and Aqua combined Moderate Resolution Imaging Spectroradiometer (MODIS), Land Cover Climate Modeling Grid (CMG) Version 6 (MCD12C1)[11] to estimate habitat change. There are 16 habitat types in MCD12C1 (under the International Geosphere-Biosphere Programme (IGBP)[26] land cover classification scheme): evergreen needle-leaf forests, evergreen broadleaf forests, deciduous broadleaf forests, mixed forests, closed shrub-lands, open shrub-lands, woody savannas, savannas, grasslands, permanent wetlands, croplands, urban and built-up lands, cropland/natural vegetation mosaics, permanent snow and ice, barren and water bodies.

MCD12C1 habitat types were used for the analysis mainly because of their relatively coarse spatial resolution and large temporal range. The spatial resolution of MCD12C1 is 0.05° (approximately 5km), which compared to the length of the routes (approximately 40km), can both detect the major habitat changes along a BBS route and exclude the noise of minor habitat changes. The

classification schemes of MCD12C1 were provided at yearly intervals across the entire globe from 2001 to 2018. Since the BBS route protocol did not change over this period,[3] we were able to use all routes with BBS records during this period giving a total number of 3014 routes (Figure S2A). A 5-km buffer was generated along each route, while the habitat change along each route was calculated by

$$\Delta H_{i,j} = \left| H_{i,j} - H_{i,j-1} \right|,$$

where $\Delta H_{i,j}$ is the absolute composition difference for habitat type i in year j, $H_{i,j}$ is the habitat composition for habitat type i in year j and $H_{i,j-1}$ is the habitat composition for habitat type i in year $j-1$. A binary habitat change index was created to indicate whether the largest change of the habitat types is for multiple magnitudes: $\geq$5% and < 10%, $\geq$10% and < 15%, $\geq$15% and < 20%, $\geq$20% and < 25%, $\geq$25% and < 30%, and $\geq$30% of the total buffer area, respectively.

To calculate whether changes of a particular habitat type are more likely to be associated with survey cessations, we estimated the cessation probability by comparing the frequency of a given habitat change type being associated with survey cessations with the frequency of that habitat change type among all habitat change types. We first classified the habitats into two categories: habitats transferring to others as donor habitats, and the habitats being transferred as recipient habitats. To measure the probability of survey cessations by a specific habitat transferring to other habitats, we defined a cessation probability for a given habitat change proportion k by

$$CP_{i,k} = \frac{n_{i,k}/n_k}{N_{i,k}/N_k},$$

where $CP_{i,k}$ is the cessation probability for a donor or recipient habitat type i, $n_{i,k}$ is the number of survey ceased (habitat change) routes by habitat type i, n_k is the total number of survey ceased (habitat change) routes, $N_{i,k}$ is the number of routes with habitat change in habitat type i, and N_k is the total number of routes with habitat change. $CP_{i,k}$approaches 0 for minimum cessation probability and increases more than 1 for higher probability.

Survey Cessation with Habitat Change

The trained recorders of the BBS were expected to record the same route for long periods of time. However, reasons that lead to an interruption of a biological survey can be varied and include age, illness, loss of interest and so forth of the surveyors.[27] Surveys that ceased by these factors might restart if another surveyor was assigned to the previous survey route. However, cessations likely caused by habitat change are more difficult to restart for the survey routes can be lost. To distinguish cessations caused by habitat change and other factors, we defined habitat-driven survey cessation as having occurred when a survey stopped and did not restart by the end of the study period (i.e., 2018). This includes three scenarios. First, habitat change may have occurred since the preceding year's survey, leading to a decision to cease a scheduled survey before it was done. Second, the prospective recorder might have observed a major habitat change when they got to the survey sites and stopped the survey. Third, surveyors might have observed a habitat change while conducting the survey and then stopped it in the following year. The first and second scenarios cannot easily be distinguished through survey records since they both show a habitat change with a survey blank in the corresponding year. Therefore, we defined the first two scenarios as immediate survey cessation and the third as later cessation. For both the immediate and later survey cessation, the survey ceased (habitat change) rate for a given proportion of habitat change (k) was calculated by $R_{HCS,k} = \frac{n_k}{N_k} \times 100\%$, where $R_{HCS}$is the survey ceased (habitat change) rate for habitat change by proportion k, n_k is the number of routes with survey ceased (habitat change) by proportion k and N_k is the number of route with habitat change by proportion k.

We also built a null spatial model to investigate the effects of survey cessation (habitat change) by randomizing the habitat change indices. Specifically, we first randomly distributed the 54108 binary habitat change indices across 3014 routes from 2001-2018, holding everything else constant, and calculated the rate of survey cessations (habitat change) with randomized habitat indices for both the immediate and later cessation. The relative survey ceased (habitat change) rate for a given proportion of habitat change (k) was calculated by $RR_{HCS,k} = \frac{sR_{HCS,k}}{rR^{HCS}_{,k}}$, where sR_k is the actual proportion of routes with habitat change by k where surveying was ceased, and rR_k is the proportion of routes with randomly distributed habitat change by k where surveying was ceased. The procedure was replicated 1000 times.

Diversity Evaluation

To make comparison with recent studies on diversity trends,[4,13] we used encountered species richness (the sum of all species at a given BBS route) for taxonomic diversity (TD). Functional (FD) and phylogenetic diversity (PD) were also calculated without weighting for abundance. For the calculation of functional diversity, we used 16 traits from Elton Traits 1.0.[28] These traits included: body mass, diet (i.e., proportional use of invertebrates, vertebrates, carrion, fresh fruits, nectar and pollen, seeds, and other plant materials in species' diet), foraging niche (i.e., prevalence of foraging below water surfaces, on water surface, on terrestrial ground level, in understory, in mid-canopy, in upper canopy, and aerial), and broad habitat types (i.e., pelagic or not), which are assumed to represent the Eltonian niche dimensions. We gave equal weights to each trait category, which resulted in 1 weight for body mass and broad habitat type and 1/7 for each diet and foraging niche variable. The functional distance was calculated using a multivariate trait dissimilarity under Gower's distance[29] for each pairwise species, followed by UPGMA clustering. Phylogenetic diversity was calculated using 100 dendrograms sampled from a full pseudo-posterior distribution of phylogenetic trees (http://birdtree.org). The mean

phylogenetic diversity across these 100 dendrograms was calculated. For each route, FD was calculated as the total lengths of the functional dendrograms of the subtree joining the observed species on a route,[30] and PD was calculated by summing up the total branch length of a sub-phylogenetic-tree joining the observed species on a route via root.[31]

We calculated overall diversity trends in two ways: the yearly change of taxonomic, functional and phylogenetic diversity between 2001-2018, and a comparison of the two extreme 3-year periods, 2001-03 and 2016-18. For the first approach, we evaluated the temporal trends in all annual metrics using general additive models (GAMs). All diversity values were scaled from 0 to 1. To account for a difference in overall diversity level among routes, we included a random effect on BBS routes. For each model, we used a loess sliding window with a 33% range width. For the second approach, we lumped 3 years to avoid the potential effect of unusual or abnormal years. We retained routes surveyed in both periods for either approach to estimate the biodiversity trend. Then for the average diversity in the 2001 and 2016 periods, the relative diversity change - $\Delta D_{2001,2016}$ - for TD, FD and PD were computed respectively by $\Delta D_{2001,2016} = \frac{D_{2016}-D_{2001}}{D_{2001}} \times 100\%$.

We estimated effects of habitat change on biodiversity by comparing diversity trends in survey continued (habitat change) routes and survey continued (no habitat change) routes. To assess the magnitude of false biodiversity trend estimation likely caused by failing to record the biodiversity loss, we simulated the diversity loss in survey ceased (habitat change) routes as different percentages of their diversity before cessation. We also simulated different percentages of survey ceased (habitat change) routes compared with the total sampled routes to quantify the extent of the potential bias. For diversity change after the assumed diversity loss, we calculated an annually relative diversity change rate in survey continued routes to simulate diversity change in survey ceased (habitat change) routes. Specifically, for each pair of consecutive year m and n in survey continued years, we calculated the estimates diversity as $\Delta D_{m,n} = \frac{D_n-D_m}{D_m} \times 100\%$.

QUANTIFICATION AND STATISTICAL ANALYSIS

All statistical analyses are performed using R 4.0.0. Statistical details related to habitat change and association with survey cessations can be found in Method details. Diversity trends are estimated by fitting general additive models (GAMs) and comparisons between the beginning and end of the study periods, and details can be found in Diversity evaluation from the Method details. Values are reported as mean value with 95% confidential intervals.

Wenyuan Zhang *, Kevin J. Gaston, Ben C. Sheldon and Richard Grenyer. (2021). Contrasting effects of rewilding, species introductions, natural colonisation and extirpation on bird and mammal diversity in the UK.

5

How novel species impact native functional diversity differently?

Contrasting effects of rewilding, species introductions, natural colonisation and extirpation on bird and mammal diversity in the UK

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Abstract

Species composition of natural assemblages varies through a range of extirpation and introduction processes. The combined effects of those processes rely on the degree to which novel species fill native functional gaps caused by species extirpation, thus balancing the lost functional diversity. We explored the effects by contrasting four mechanisms for change in community composition - species introduction, unassisted colonisation, rewilding and extirpation – in terms of their impacts on the functional diversity of birds and mammals in the UK. By adding novel species to the extant native species pool, we calculated diversity changes and quantified overlaps in functional trait space. We show that: (i) introduced/naturalised birds contribute more functional uniqueness to native functional space than other groups of birds; (ii) functional diversity change caused by 'rewilded' species was species-dependent and idiosyncratic, whilst rewilding mammals contributed least in terms of functional uniqueness to existing functional space; and (iii) mammals and birds differed in the influence of extirpated species, with extirpated mammals contributing more functional diversity and functional uniqueness than for birds. Our results suggest that although rewilding in the UK can expand or infill native functional trait space, such effects of specific programmes may need careful assessment.

Keywords: alien species; conservation translocation; ecosystem restoration; hypervolume analysis; rewilding; species reintroduction.

Introduction

Biodiversity has undergone fundamental alteration worldwide (Simberloff *et al.*, 2013; Lewis & Maslin, 2015), which largely impacts the functioning of ecosystems with uncertain outcomes. On the one hand, species extirpation often comes with a disproportionate loss of evolutionary history and functional traits, causing the perturbations of some key ecosystem functions (Gaston & Blackburn, 1995; Smith *et al.*, 2018). On the other hand, novel species may outnumber extirpated species at a local scale (Dov F. Sax *et al.*, 2002), potentially buffering functional diversity loss. Therefore, it is important to understand the different effects of processes that result in turnover of species in ecological communities, and how introduction of novel species can compensate for the loss of extirpated species.

Four processes can cause variation in the species composition of natural assemblages, i.e., extirpation, intentional/accidental human introduction, rewilding and unassisted (re)colonisation, which may have different effects on native diversity. Non-native species are thought to be a major threat to native diversity and can cause extirpations through predation and competitive displacement, which leads to global diversity loss (Simberloff *et al.*, 2013; Pimm *et al.*, 2014; Dawson *et al.*, 2017; Catford *et al.*, 2018). However, it has been demonstrated that non-native species could be tolerated and used for ecosystem restoration where they could play positive ecological roles (Ewel & Putz, 2004). Despite major efforts to determine the effects of species introduction on native diversity, how these effects differ from each other remains challenging.

Particularly, to stem the loss of biodiversity, rewilding, a special case of species (re)introduction, has been proposed to (re-)establish species that existed before ecosystems were profoundly altered by human impacts (Perino *et al.*, 2019). The key definitions of rewilding have developed in the last decades, and current focus of rewilding today is on species (re)introduction as a way to restore ecosystem functioning (Nogués-Bravo *et al.*, 2016). Nevertheless, it has been criticised for lacking knowledge about its potential outcomes (Nogués-Bravo *et al.*, 2016). One such lack is understanding the influence of rewilding projects on filling functional gaps in extant native species pools. Although rewilding programmes have been executed and proposed on the grounds, at least in part, that the reintroduction of extirpated species will have such outcomes, whether they do so remains largely untested.

In addition, theories that tried to explain the ecological similarities between new colonists and native species also seem contradictory. The most well-known are Darwin's two competing naturalisation hypotheses (i.e., Darwin's naturalisation conundrum) – the *preadaptation naturalisation hypothesis* and the *competition-relatedness naturalisation hypothesis* (Darwin, 1928; Curtis C. Daehler, 2001). According to Darwin's preadaptation naturalisation hypothesis, non-native species closely related to native species would be more likely to colonise naturally, given their potentially similar adaptations to the local environments they shared with native species. In this case, the non-native colonists might add few functional traits or evolutionary history that were not already present in native assemblages of species. However, an opposite outcome might result from the competition-relatedness naturalisation hypothesis, where a lack of competitive exclusion would facilitate the establishment of alien species that are

phylogenetically and functionally distinct from native species (Park *et al.*, 2020). Thus, non-native colonists might also contribute marked functional uniqueness and evolutionary history to native assemblages of species.

In summary, the different effects of rewilding, species introduction, extirpation and unassisted colonisation on native diversity are unclear; conservation policy regarding how to deal with species with different kinds of origins is also consequently debated (Sax & Brown, 2000; Mačić *et al.*, 2018). Disentangling the effects of rewilding, species introduction, extirpation and unassisted colonisation on native diversity is therefore a critical step in limiting the future risks of inappropriate conservation practices. Here, we contrast impacts of species introduction, natural colonisation, and rewilding on extant functional and phylogenetic diversity for birds and mammals in the UK. We estimate (1) how adding individual and groups of novel species (i.e., introduced, naturalised, naturally colonised, extirpated and rewilding species) quantitatively changes extant native functional and phylogenetic diversity, and (2) the extent to which different groups of novel species differ from native species in functional trait space.

Materials and Methods

Summary

We estimated the different effects across five groups of novel species: (i) *introduced species* – species that were introduced by humans and have bred in the wild without establishing self-sustaining populations; (ii) *naturalised species* – those that have established populations derived from the human introduction; (iii) *recent (re)colonists* –

those that have colonised (or re-colonised) naturally without direct human interference; (iv) *rewilding species* – those that are being reintroduced and reinforced by human-mediated conservation translocation; and (v) *extirpated species* – those that are extinct in the UK, but exist elsewhere.

We tested the influence of the five groups of novel species on extant native diversity through two processes. First, we quantified how much functional and phylogenetic diversity increased when adding different individual/groups of novel species to the native species pool. Second, we measured how different groups of novel species overlap with native species in functional trait space using a hypervolume method, with which we estimated how much functional uniqueness the novel species could contribute to native assemblages of species.

Bird and mammal data

We built a bird list using data from the Avian Population Estimates Panel (APEP4) (Woodward *et al.*, 2020) for the diversity evaluation. Given that wintering species have less site fidelity than breeding species and the effects of non-breeding on local diversity are therefore unstable (Matthiopoulos *et al.*, 2005), we excluded wintering species for the subsequent analyses. We also employed the British List (BOU, 2018) to categorise introduced, naturalised, recent colonised, extirpated and rewilding species. Specifically, we added the species that have already bred in the wild but are not judged to be self-sustaining on the British List as introduced species. The naturalised species are those that were included in APEP4 and listed as naturalised species on the British List. We defined

the recent (re)colonists as species that have colonised since 1945. We classified species that are being reintroduced and reinforced by human-mediated conservation translocation as rewilded species, for which we collated data from multiple sources (See Table S1 for details).

One challenge in assessing the effect of human interference on species assemblages is that some species have multiple possible categorisations at the scale of the UK, a problem that will also occur at other national and larger scales. This is particularly the case where relict populations have been supplemented elsewhere by reintroductions, or wild populations have been supplemented by captive releases. In order to capture these multiple categorisations we ran analyses twice, with each such species classified with the focus on either (i) natural processes or (ii) anthropogenic processes. Specifically, under the natural classification, species that have populations from both direct human interference and natural processes are categorised to the group that is more related to human interference, so that the remaining species whose populations are all derived from natural processes (i.e., recent colonists and native species) are in a group distinct from those with mixed populations. For example, we classify the red kite *Milvus milvus* as a rewilding species under the natural classification, given the reintroduced populations (first in Chilterns in southern England and then in the East Midlands, central Scotland and Yorkshire), despite its native populations in mid-Wales (Wotton *et al.*, 2002). The common crane *Grus grus* is also categorised as a rewilding species under the natural classification, considering that its population in the UK includes some parts that derive from rewilding projects (e.g. in Southwest England; thegreatcraneproject.org.uk), although other parts are derived from natural recolonisation (initially centred on Norfolk)

(Gibb *et al.*, 2021). Under the anthropogenic classification, species that have populations from both direct human interference and natural processes are categorised to the group that is less related to human interference (i.e., recent colonists and native species). Thus, under the anthropogenic classification, we classify common crane and red kite as a recent colonist and a native species, respectively; other species with mixed categorisation include greylag goose *Anser anser*, mallard *Anas platyrhynchos*, corncrake *Crex crex*, cirl bunting *Emberiza cirlus*, black-tailed godwit *Limosa limosa*, osprey *Pandion haliaetus*, grey partridge *Perdix perdix*, barn owl *Tyto alba*, rock dove *Columba livia* and northern goshawk *Accipiter gentilis*.

We used the UK Mammal List from the Mammal Society (Crawley, 2020) for the analysis of the mammal fauna, using the classification of extant native species in this list. Introduced and naturalised species were in the same category in the mammal list, and we separated them based on Macdonald and Burnham (2010). We derived the list of rewilding species from related project websites (see Table S2 for details). There are no recent (re)colonised mammals in the UK, so that category does not exist in the mammal analysis. We also excluded pinnipeds and cetaceans. For both birds and mammals, we determined the extirpated species based on Yalden and Barrett (1999) and Yalden and Albarella (2008) since the Late Glacial Maximum (around 12,000 years ago) when the British Isles began to be cut off from the continent, and the ice retreated and re-opened the North Sea and the English Channel.

Overall, we classified 248 bird species, of which the natural classification comprised 173 native species, 26 introduced species, 18 naturalised species, 11 recent (re)colonists, 6 extirpated species and 14 rewilding species, whilst the anthropogenic classification comprised 186 native species, 26 introduced species, 12 naturalised species, 13 recent (re)colonists, 6 extirpated species and 5 rewilding species (See Table S1 for full list). We categorised 76 mammal species, consisting of 43 native species, 2 introduced species, 12 naturalised species, 7 rewilding species and 12 extirpated species (See Table S2 for full list).

Diversity

To quantify diversity change, we calculated functional and phylogenetic diversity based on abundance unweighted methods. We used five traits to calculate functional diversity: body mass, litter/clutch size, generation length, foraging strata of birds/habitat breadth of mammals (number of IUCN habitats listed as suitable) and diet (Wilman *et al.*, 2014; Bird *et al.*, 2020; Soria *et al.*, 2021). These traits reflect the resource acquisition, utilisation and release by species and thus summarise their major ecological function (Petchey *et al.*, 2004; Flynn *et al.*, 2009; Newbold *et al.*, 2013; Cooke *et al.*, 2019). The foraging strata and diet classification are ordinal categorical variables with seven levels. Specifically, the foraging stratum is the proportion of foraging below water surfaces, on the water surface, on terrestrial ground level, in the understory, in mid-canopy, in upper canopy and aerial, whilst the diet is the proportion of invertebrates, vertebrates, carrion, fresh fruits, nectar and pollen, seeds, and other plant materials in species' diet. We then calculated the functional distance using a multivariate trait dissimilarity of Gower's distance (Gower, 1971) for each pairwise species, followed by Unweighted Pair Group

Method with Arithmetic Mean (UPGMA) clustering. Functional diversity was calculated as the summed branch lengths of the functional dendrogram (Petchey & Gaston, 2002). Phylogenetic distance was calculated using 100 dendrograms sampled randomly from a full pseudo-posterior distribution of phylogenetic trees (http://birdtree.org). The mean phylogenetic diversity across these 100 dendrograms was calculated, and phylogenetic diversity was taken as the sum of the total branch length of a phylogenetic tree via the root (Faith, 1992).

We assessed the influence of the novel species (i.e., introduced, naturalised, recently (re)colonised, rewilding and extirpated species) on native diversity by first calculating the native functional and phylogenetic diversity, and then the diversity change after adding each individual/group of the novel species. For individual novel species i, we scaled diversity changes d_i from 0 to 1 using $D_i = \frac{d_i - \min(d)}{\max(d) - \min(d)}$, where D_i is the standardised diversity change for species *i*, min(d) is the minimum of all diversity changes, and max(d) is the maximum of all changes. For each novel species group g, we used a relative diversity change RD_g to measure the difference between native species and the assemblages that combined native and novel species, $RD_g = \frac{CD_g - ND}{ND}$ where ND is the native diversity and CD_g is the combined diversity.

Hypervolume estimation

We used hypervolume analysis to estimate how different groups of introduced, naturalised, recent (re)colonised, rewilding and extirpated species overlap with native species in the functional trait space (i.e., how much functional uniqueness the novel

species contribute to native species). The hypervolume approach is a way to measure accurately the volume of a high-dimensional shape without assuming a parametric probability distribution (Blonder, 2018) and can capture holes, disjunctions or other complex geometrical features. A hypervolume models multidimensional spaces better than linear and continuous dimensions, such as convex hulls (Cornwell *et al.*, 2006), and can be used to measure the overlap of different species in functional trait space (Cooke *et al.*, 2019).

We first built a hypervolume for each group of novel and native species using the one-class Support Vector Machine (SVM) estimation method (Blonder, 2018; Cooke *et al.*, 2019). SVM provides a smooth fit around the data that is robust to outliers, yields a binary boundary classification ('in' or 'out'), is invariant to rotational transformation (i.e. correlations between axes), and is computationally viable in large datasets and high dimensional hyperspaces (Blonder, 2018). We calculated the observed hypervolume based on the transformed and standardised traits using the 'hypervolume_svm()' function in the hypervolume package (Blonder *et al.*, 2014; Blonder, 2018). Analyses with few observations are likely to be biased and not recommended for hypervolume anlysis (Blonder *et al.*, 2014), so we excluded the results when the number of species within a given group is less than the number of traits.

We then assessed pairwise overlap among the hypervolumes using the 'hypervolume_overlap_statistics' function in the 'hypervolume' package, which calculates the unique and overlapped volume fraction of each pair of hypervolumes

(Blonder & Harris, 2019). Specifically, we assessed pairwise overlap between native species and each group of introduced, naturalised, recent (re)colonised, rewilding and extirpated species (five paired hypervolumes in total), and so we used the fraction of functional space that was not occupied by native species to evaluate the functional uniqueness that groups of novel species contributed to native assemblages of species. Whilst comparative statistics are influenced by sample size (Blonder, 2018), we were interested in the total volume of trait space occupied by each introduced, naturalised, recent (re)colonised, rewilding and extirpated species relative to the entire trait space occupied by native species, and thus we used the original sample size in this analysis.

In contrast to the calculation of functional diversity, the hypervolume analysis needs traits that belong to the same category to be on one axis. Therefore, we calculated continuous measures for a species' diet and foraging strata based on semi-quantitative records of seven diet and seven foraging strata categories. We first calculated Gower Distance (Gower, 1971) between species based on the diet or foraging strata data following a principal component analysis (PCoA). PCoA retains the positions of the species relative to each other but changes the coordinate system. Trait space and hypervolume analyses assume that contributions to distances and volumes are equal for axes (Blonder, 2018). Therefore, we used the first principal component as synthetic trait values in the trait space and hypervolume analyses, which capture 38.6% of the diet and 41.1% of foraging strata variation for birds, and 53.4% of diet variation for mammals. This represents the relative importance of diet or foraging strata in the initial dataset (Cooke *et al.*, 2019). Conversion to unitless coordinates is required so that volumes or overlaps can be defined. We therefore first transformed trait data to improve normality: $\log_{10}$ for body mass,

generation length and litter/clutch size and square root for habitat breadth; we then standardised all traits to zero mean and unit variance (z-transformation). The units of the hypervolumes are reported as the standard deviations of centred and scaled transformed trait values, raised to the power of the number of dimensions (SD number of dimensions).

Results

We found that while the influence of the novel species on extant native diversity varied considerably within and across each group, there were general patterns. In summary, (i) introduced/naturalised bird species contributed the most functional uniqueness to native functional space compared to other groups of birds; (ii) functional diversity change caused by rewilding species was largely influenced by whether certain individual species were included, whilst rewilding mammals contributed less functional uniqueness to native functional space than other groups of mammals; and (iii) reintroducing extirpated mammals would increase native diversity relatively more and contribute more functional uniqueness than in the case of birds.

For individual bird species, we found the greatest increase in functional diversity when adding common crane *Grus grus*, great bustard *Otis tarda*, Dalmatian pelican *Pelecanus crispus* and Eurasian golden oriole *Oriolus oriolus* to native assemblages of avian species, whilst cirl bunting *Emberiza cirlus*, Temminck's stint *Calidris temminckii*, Harris's hawk *Parabuteo unicinctus* and northern goshawk *Accipiter gentilis* were the four species that increased native bird functional diversity least (Figure 1-A and 2-A). In contrast to functional diversity, the greatest increase in phylogenetic diversity was found, perhaps

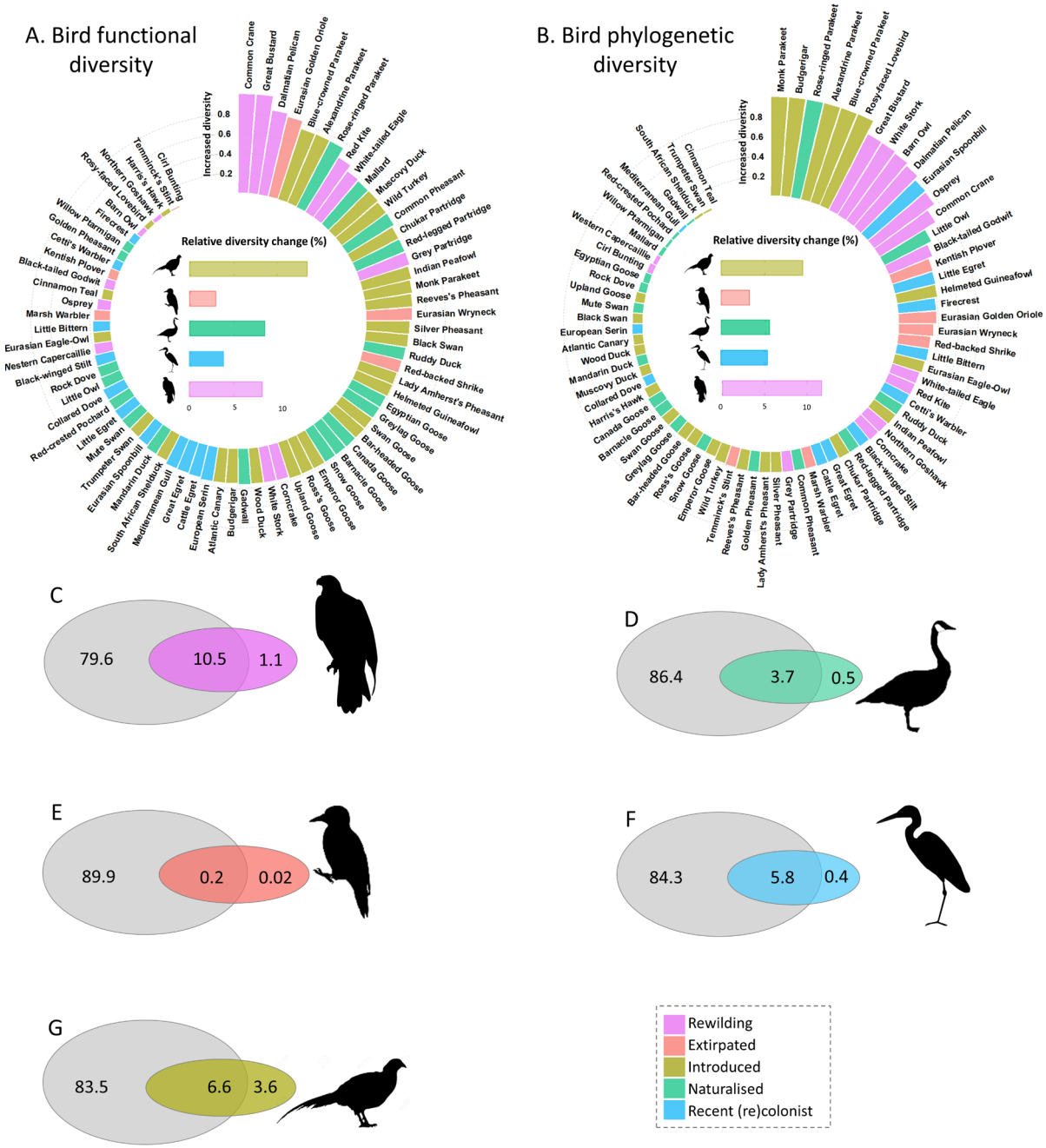

Figure 1. Influence of introduced, naturalised, recent (re)colonised, rewilding and extirpated species on native bird diversity based on natural classification. Bar height

indicates the increase in native **(A)** functional and **(B)** phylogenetic diversity when adding an individual introduced, naturalised, recent (re)colonised, rewilding or extirpated species to native assemblages of species, standardised to vary from 0 to 1. Different colours represent different groups of introduced, naturalised, recent (re)colonised, rewilding and extirpated species. **(C)-(G)** Two-dimensional representation of the overlap in five-dimensional trait space. Different colours represent different groups of species: native species (grey, full volume ~92 SD^5), introduced species (yellow, full volume ~10 SD^5), naturalised species (turquoise, full volume ~5 SD^5), recent (re)colonists (blue, full volume ~6 SD^5), rewilding species (purple, full volume ~6 SD^5), and extirpated species (red, full volume ~0.4 SD^5). Hypervolumes for each group of species were constructed on the basis of five z-transformed traits: log10(body mass), log10(clutch size), log10(generation length), diet and foraging strata. The units of the unique and overlapping fractions are SD^5. Bird silhouettes give examples of different groups of introduced, naturalised, recent (re)colonist, rewilding and extirpated species and were freely downloaded from PhyloPic (www.phylopic.org), under CC0 1.0 Publica Domain Dedication.

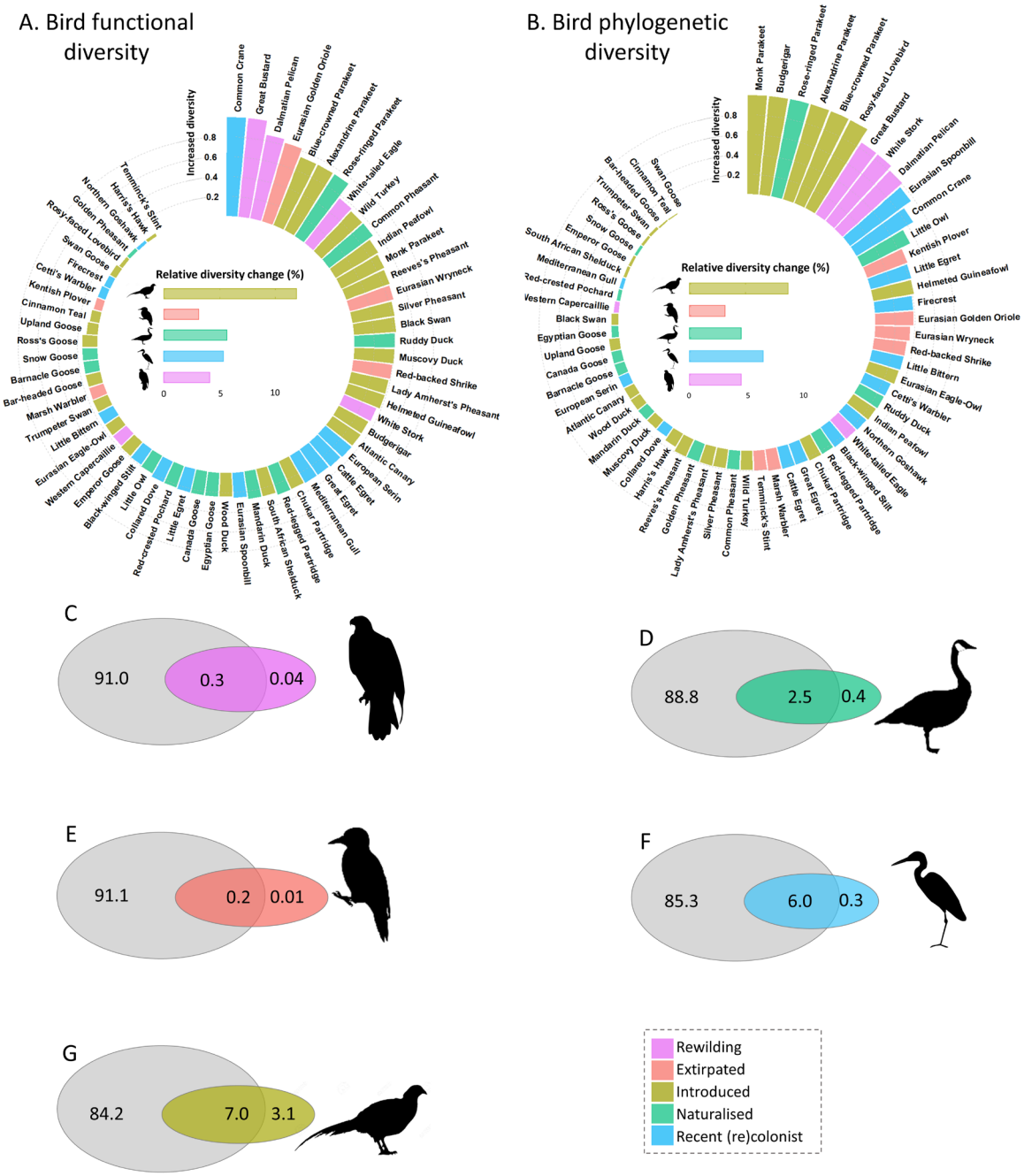

Figure 2. Influence of introduced, naturalised, recent (re)colonised, rewilding and extirpated species on native bird diversity based on anthropogenic classification. Bar

height indicates the increase in native **(A)** functional and **(B)** phylogenetic diversity when adding an individual introduced, naturalised, recent (re)colonised, rewilding or extirpated species to native assemblages of species, standardised to vary from 0 to 1. Different colours represent different groups of introduced, naturalised, recent (re)colonised, rewilding and extirpated species. **(C)-(G)** Two-dimensional representation of the overlap in five-dimensional trait space. Different colours represent different groups of species: native species (grey, full volume ~93 SD^5), introduced species (yellow, full volume ~10 SD^5), naturalised species (turquoise, full volume ~4 SD^5), recent (re)colonists (blue, full volume ~6 SD^5), rewilding species (purple, full volume ~0.4 SD^5), and extirpated species (red, full volume ~0.4 SD^5). Hypervolumes for each group of species were constructed on the basis of five z-transformed traits: log10(body mass), log10(clutch size), log10(generation length), diet and foraging strata. The units of the unique and overlapping fractions are SD^5. Bird silhouettes give examples of different groups of introduced, naturalised, recent (re)colonist, rewilding and extirpated species and were freely downloaded from PhyloPic (www.phylopic.org), under CC0 1.0 Publica Domain Dedication.

unsurprisingly, when monk parakeet *Myiopsitta monachus*, budgerigar *Melopsittacus undulatus*, rose-ringed parakeet *Psittacula krameri* and Alexandrine parakeet *Psittacula eupatria* were added to native assemblages, while swan goose *Anser cygnoides*, cinnamon teal *Anas cyanoptera*, bar-headed goose *Anser indicus* and trumpeter swan *Cygnus buccinator* had the smallest effect on phylogenetic diversity (Figure 1-B and 2-B). For mammals, European bison *Bison bonasus*, wolverine *Gulo gulo*, brown rat *Rattus norvegicus* and wild boar *Sus scrofa* would contribute the most growth in functional diversity when adding individual mammal species to the native species pool; the European bison had nearly twice the effect on functional diversity as the following most influential species, the wolverine (Figure 3-A). Red-necked wallaby *Macropus rufogriseus*, greater mouse-eared bat *Myotis myotis*, Chinese water deer *Hydropotes inermis* and root vole *Microtus oeconomus* had the most minor effects on native functional diversity. In contrast, whilst adding red-necked wallaby to native mammal assemblages had the smallest effect of any species on functional diversity, unsurprisingly, as the only non-eutherian mammal, it caused the largest change in phylogenetic diversity - approximately five times the effect of the following most influential species, the feral horse (Exmoor/Dartmoor pony *Equus ferus caballus* Figure 3-B). Adding Eurasian beaver *Castor fiber* and wild boar *Sus scrofa* to native mammal assemblages resulted in the third and fourth greatest growth in phylogenetic diversity, whilst adding Sika deer *Cervus nippon*, brown hare *Lepus europaeu*s, Arctic fox *Vulpes lagopus* and root vole *Microtus oeconomus* had the smallest increase.

When considering the effect of groups of species, we found functional diversity of avian assemblages increased most when adding introduced species to the native bird

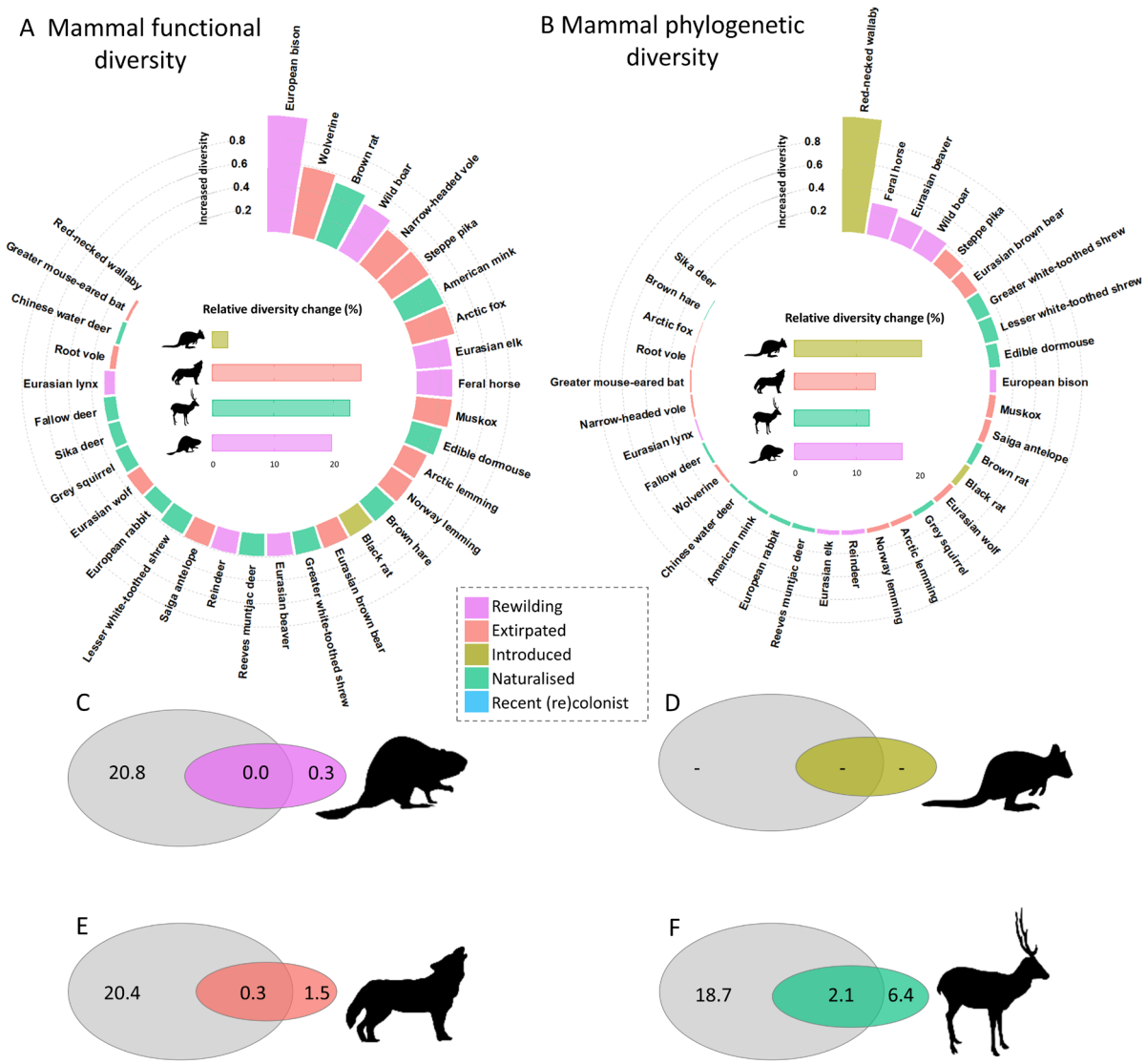

Figure 3. Influence of introduced, naturalised, recent (re)colonised, rewilding and extirpated species on native mammal diversity. Bar height indicates the increase in native **(A)** functional and **(B)** phylogenetic diversity when adding an individual introduced, naturalised, recent (re)colonised, rewilding or extirpated species to native assemblages of species, standardised to vary from 0 to 1. Different colours represent

different groups of introduced, naturalised, recent (re)colonised, rewilding and extirpated species. **(C) - (F)** Two-dimensional representation of the overlap in five-dimensional trait space. Different colours represent different groups of species: native species (grey, full volume ~20 SD^5), introduced species (yellow, full volume not available as a number of species is less than the number of traits), naturalised species (turquoise, full volume ~9 SD^5), rewilding species (purple, full volume ~ 0.3 SD^5), and extirpated species (red, full volume ~3 SD^5). Hypervolumes for each group of species were constructed on the basis of five z-transformed traits: log10(body mass), log10(clutch size), log10(generation length), sqrt(habitat breadth) and diet. The units of the unique and overlapping fractions are SD^5. Mammal silhouettes give examples of different groups of introduced, naturalised, rewilding and extirpated species and were freely downloaded from PhyloPic (www.phylopic.org), under CC0 1.0 Publica Domain Dedication.

assemblages (under both natural and anthropogenic classifications; Table 1); relative increased functional diversities were 13.7% and 11.9% respectively (Figure 1-A and 2-A). Introduced species increased phylogenetic diversity most (by 8.8%) under the anthropogenic classification, whilst rewilding species increased phylogenetic diversity the most under the natural classification (by 11.5%; Figure 1-B and 2-B). Under the natural classification, 14 rewilding species increased bird functional diversity by 8.6% and phylogenetic diversity by 11.5% (Table 1). The effects became smaller under the anthropogenic classification, with the five rewilding species increasing functional diversity by 4.1% and phylogenetic diversity by 4.6%. Adding naturalised species increased the functional diversity of native bird assemblages by more than adding recent (re)colonists in both anthropogenic and natural strategies, whilst adding naturalised species increased native phylogenetic diversity by more in the natural classification and less in the anthropogenic classification than adding recent (re)colonists. Extirpated bird species caused the least growth in functional and phylogenetic diversity for both anthropogenic and natural strategies when adding them to native bird assemblages.

Reintroducing extirpated mammals would have the largest effect on functional diversity compared to other groups of novel mammal species (25.3% relative diversity growth), whilst introduced species had the smallest effect (2.6% relative diversity growth) (Figure 3-A). Only two mammal species were classified as introduced and increased the phylogenetic diversity of native species the most (21.6% relative diversity growth) (Figure 3-B). Whilst adding naturalised species to the native mammal assemblage increased functional diversity by the second largest amount (23.6% relative diversity

change), it contributed the least growth in phylogenetic diversity (13.0%). The functional diversity of the native mammal assemblage increased 20.3% by adding rewilding species.

We found that introduced bird species had the largest functional trait space that was unoccupied by native bird species for both natural (unique volume = 3.6 SD^5) and anthropogenic (unique volume = 3.1 SD^5) classifications (Figure 1 C-G and Figure 2 C-G). Rewilding birds have the second least space that is not occupied by native species based on the anthropogenic classification (0.05% of the combined volume 91.3 SD^5), and the second largest functional trait space unoccupied by native bird species for the natural classification (1.2% of the combined volume 91.1 SD^5). For both classifications, extirpated species have the least unique space compared with native species (0.02% of the combined volume 90.1 SD^5 under anthropogenic classifications, and 0.01% of the combined volume 91.3 SD^5 under anthropogenic classifications). Naturalised species occupied 0.5% and 0.4% of combined space unoccupied by native species for natural (unique volume = 0.5 SD^5) and anthropogenic (unique volume = 0.4 SD^5) classifications respectively, followed by recent (re)colonists (unique volume = 0.4 SD^5 under natural classifications and 0.3 under anthropogenic classifications). Recent (re)colonists had the largest proportion of overlap with native bird species in functional trait space for both classifications. The overlap space accounts for 94.2% (intersection volume = 5.8 SD^5) of the functional trait space of recent (re)colonists for the natural classification (full volume = 6.2 SD^5), whilst this value for the anthropogenic classification was 95.3% (full volume = 6.3 SD^5).

Compared with birds, mammals had different patterns of relative occupation of functional trait space by groups (Table 1). Naturalised mammal species had the largest space that was not occupied by native species (unique volume = 6.4 SD^5). Rewilding mammals had the least space unoccupied by native species (unique volume = 6.4 SD^5) and least overlap with native species (intersection volume = 0.0 SD^5). Extirpated mammal species occupied 6.8% of space (unique volume = 1.5 SD^5) unoccupied by native species (combined volume 22.3 SD^5).

Discussion

We contrast the effects of four mechanisms for change in community composition - species introduction, rewilding, unassisted colonisation and extirpation – in terms of their impact on the functional and phylogenetic diversity of birds and mammals in the UK. By adding different individual species and groups of novel avian and mammalian species (i.e., introduced, naturalised, recent (re)cent colonised, rewilding and extirpated species) to the native assemblages of species, we show that the species that currently comprise rewilding options in the UK contribute less functional uniqueness than those brought in by human introduction, and the overall effects of rewilding on filling functional gaps are species-specific and idiosyncratic. Bird natural (re)colonists share the most similar functional traits with extant native bird species but also contribute more functional uniqueness than the species which have been extirpated from the UK. Reintroducing extirpated species would have a larger effect on the functional diversity of mammals than on birds.

We found that both the rewilding bird and mammal species increase functional diversity by less, and contribute less functional uniqueness, than naturalised and introduced species. This indicates that human introductions of species tend to include species with more dissimilar functional traits than native species, perhaps because their 'exotic' nature is a common driver for the processes that lead to introductions. Conservation targets aiming at filling functional gaps thus might not be most effectively addressed by rewilding programmes as they are currently envisaged. On the other hand, we found that rewilding birds contributed more functional uniqueness to extant native species than recent (re)colonists under the natural classification. These results suggest that an intervention approach is still important if filling functional gaps is a goal. This can be viewed from two perspectives. First, recent (re)colonists shared more functional traits with extant native species, suggesting that birds experiencing natural colonisation are more likely to follow the preadaptation naturalisation hypothesis, so that their trait combinations have not filled much of the niche of extant native species. Second, rewilding, as a human-mediated approach, worked better than natural colonisation in filling functional gaps. This emphasises that some distinct niches in functional space were filled by rewilding species, which, in total, are morphologically diverse and cannot be filled by the process of natural colonisation. Likewise, rewilding birds contributed more functional uniqueness than extirpated birds, which also suggests that rewilding programmes were trying to reintroduce more functionally distinct species, so extirpated species with less distinct functional traits have not been reintroduced in rewilding programmes.

Recent and potential community changes differ between mammals and birds, most notably in the effects of reintroducing extirpated species. Reintroducing extirpated bird

species increases the functional diversity of native assemblages relatively little, whilst reintroducing extirpated mammals could contribute more functional uniqueness than rewilding mammals. These outcomes could potentially be explained as a consequence of the large variance in individual-level functional traits in rewilding species, i.e. although some rewilding species could increase functional diversity by more than other species (e.g., common crane and European bison), a half of rewilding species increase it by less (e.g., northern goshawk and Eurasian lynx). This also highlights the necessity to assess the species-dependent effects for rewilding projects if filling functional gaps is the principle aim. For example, reintroducing Dalmatian pelican (proposed by the Wildlife Trusts - wildlifetrusts.org) and Eurasian golden oriole (recently extinct in the UK) would cause the largest increase in functional diversity for birds, whereas reintroducing Eurasian wolf would increase functional diversity for mammals least.

In parallel with functional diversity, we found that species-dependent effects on phylogenetic diversity tend to be stronger than that on functional diversity. Two introduced mammal species (Red-necked wallaby *Macropus rufogriseus* and Black rat *Rattus ratt*us) increased the most native phylogenetic diversity. This suggests that even a limited number of species with distinct evolutionary histories can largely influence phylogenetic diversity. In addition, introduced species increased native phylogenetic diversity more than rewilding species for birds under the anthropogenic classification. This implies that while rewilding birds and mammals also tend to be more evolutionarily distinct than by chance (Thévenin *et al.*, 2018), their potential contribution to phylogenetic diversity does not exceed introduced species. The results corroborate our previous conclusions on functional diversity that rewilding programmes overall may be

not particularly effective for the conservation targets of increasing the native functional and phylogenetic diversity, and the species-dependent effects should be considered.

The UK is characterised by having comparatively well-known assemblages of species as well as non-trivial numbers of naturalised species and several rewilding projects underway or proposed. However, the results here may also have implications for other regions in terms of the importance of considering species-dependent effects if rewilding programmes are proposed. We also showed that the contribution of rewilded species could be very dependent on how species with more complicated local histories (archaeo-introductions, population reinforcement, and uncertain reproductive status) are viewed.

Rewilding is usually driven by national conservation targets and the ability to garner public and political support (Thévenin *et al.*, 2018). It is of critical importance to evaluate the effects of rewilding programmes before implementation, especially when rewilding as a conservation discipline comprises significant unknowns in the ecological and socio-economic realms (Nogués-Bravo *et al.*, 2016). Our results show that although rewilding in the UK could have more positive effects than natural colonisation in terms of expanding or infilling functional trait space of extant native species, the effects are largely species-dependent. Our results provide important insights for the much-discussed conservation translocation rewilding programmes (Lorimer *et al.*, 2015; Rubenstein & Rubenstein, 2016; Svenning *et al.*, 2016), and we suggest that rewilding programmes require careful assessments if filling the functional gaps is a goal.

Table 1. Effects of introduced, naturalised, recent (re)colonist, rewilding and extirpated species on extant native diversity measured by functional diversity, phylogenetic diversity and hypervolume space.

	Classification	Measures	Introduced	Naturalised	Recent (re)colonist	Rewilding	Extirpated
Birds	Natural	Number of species	26	18	11	14	6
		Increased functional diversity (%)	13.7	8.9	4.1	8.6	3.1
		Increased phylogenetic diversity (%)	9.7	5.7	5.5	11.5	3.4
		Unique functional space (SD^5)	3.6	0.5	0.4	1.1	0.02
	Anthropogenic	Number of species	26	12	13	5	6
		Increased functional diversity (%)	11.9	5.3	5.3	4.1	2.9
		Increased phylogenetic diversity (%)	8.8	4.5	6.7	4.6	3.2
		Unique functional space (SD^5)	3.1	0.4	0.3	0.04	0.01
Mammals		Number of species	2	12	0	7	12
		Increased functional diversity (%)	2.6	23.6	-	20.3	25.3
		Increased phylogenetic diversity (%)	21.6	13.0	-	18.4	13.7
		Unique functional space (SD^5)	-	6.4	-	0.3	1.5

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6

General Discussion

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Aims and Motivation

The patterns, drivers and consequences of biodiversity change, both in specific locations and across the globe, are central and compelling aspects of ecology and evolution (Gaston, 2000; Cardinale *et al.*, 2012; McGill *et al.*, 2019). Due to modern technological and computational advances allowing tracking and quantification of biodiversity patterns of various taxa (Taberlet *et al.*, 2018; Worm & Tittensor, 2018), numerous breakthroughs have recently been made in terms of the levels, patterns and structure of, and values derived from, biodiversity (Faith, 1992; Petchey & Gaston, 2002; Tilman *et al.*, 2006; Turner *et al.*, 2007; Jackson & Sax, 2010; Mace *et al.*, 2012; Winter *et al.*, 2013; Tilman *et al.*, 2014; Oliver *et al.*, 2015; Soto-Navarro *et al.*, 2021). In particular, this comes with challenges of global ecological change, such as habitat destruction (Tilman *et al.*, 1994; Tilman & Lehman, 2018), climate change (Karl & Trenberth, 2003; Thomas *et al.*, 2004; Lewis, 2006; Román-Palacios & Wiens, 2020), diversity decline (Dawson *et al.*, 2011; Davis *et al.*, 2018; Pascual *et al.*, 2021) and global epidemic (IPBES Secretariat, 2020). Therefore, it becomes increasingly important to provide reliable descriptions and explanations of diversity patterns for informed decision-making and effective conservation planning. This requires consistent, long-term monitoring data and helpful estimation of species status and distribution. Gaps in diversity estimation can prevent accurate reporting on the condition of ecological systems and hinder the identification of biodiversity vulnerability (Wilson & Roberts, 2011; Harrison *et al.*, 2014).

In this thesis, I have explored multiple perspectives on biodiversity estimation and its implications. Motivated by divergent inferences on whether overall local species richness is declining (Cardinale *et al.*, 2018) and potential biases in diversity estimation due to a lack of systematic data collection across the globe (Desquilbet *et al.*, 2021; Hughes *et al.*, 2021), I constructed and employed spatially neutral community models and longitudinal diversity survey data to examine the impacts of various factors (i.e., spatial sample coverage and scale, human-nature interaction, geographic structure) that may influence diversity estimation. By contrasting impacts of rewilding, species introduction, unassisted colonisation and extirpation on extant native diversity, I also aimed to assess the effects of conservation translocation, i.e., rewilding, especially whether they could infill the functional gaps of extant native assemblages effectively as proposed.

The integrity in diversity estimation

Spatial heterogeneity and temporal dynamics are two fundamental perspectives of biodiversity (Gaston, 2000; Pereira *et al.*, 2012), shaping our understanding of biodiversity. This requires diversity estimation to account for the effects of spatial and temporal integrity to provide robust inferences over a planetary extent. The spatial and temporal integrity can be defined as adequate sampling effort and continuity, accurate sampling strategy and scale, and proper data synthesis approaches to capture diversity change in a given landscape.

To account for spatial heterogeneity and its role in biodiversity, fundamental research from around the beginning of the 21st century has begun to focus on how sampling strategies

could influence diversity estimation across different ecosystems (Underwood, 1996; Loreau, 1998; Yesson *et al.*, 2007; DeWan & Zipkin, 2010; Chase *et al.*, 2019), such as forest (Gimaret-Carpentier *et al.*, 1998), groundwater (Dole-Olivier *et al.*, 2009), ocean (Montes *et al.*, 2021) and urban ecosystems (Callaghan *et al.*, 2019). However, it remains a preeminent challenge to assess how spatial sampling coverage, scales and structure influence the diversity estimation.

In this thesis, I examine how spatial sample coverage and scale may reconcile divergent inferences on whether local diversity is declining across the globe (**Chapter 2)**, which is a central challenge in global diversity trend estimation and essential for conservation (Cardinale *et al.*, 2018). Through constructing spatially neutral community models, I illustrate that in a virtual landscape with global diversity decline, the overall diversity trends estimated by local species richness can still increase if the spatial sample coverage is limited. Further, I show imprecise sampling scales can also contribute to the biased diversity trend estimation (**Chapter 2**). In related work, based on approaches of multiple spatial scales, **Appendix F** demonstrates that waterbird diversity along the Yangtze River is influenced by not only the central habitat but also the surrounding landscape that they rarely used.

The relationship between spatial structure and long-term diversity change is investigated in **Chapter 3**. By assessing whether diversity time-series that have similar behaviour in temporal variability are spatially independent, I show that geographic proximity does not necessarily account for patterns of diversity change. The distribution of diversity time-series that have similar temporal variation may be random. Therefore, whilst geographic structure,

such as the ecoregion and biome, has been used to delimit diversity patterns for a long time (Jetz *et al.*, 2012; Rich & Currie, 2018; Smith *et al.*, 2018), this work confirms other important forms of relationship between the two. The geographic structure does not necessarily align with diversity patterns in the case where dynamic diversity changes rather than the static diversity distribution is used to recognise North American bird diversity patterns. The findings indicate that despite geographic proximity of diversity distribution in Euclidean space, the case containing time as an extra dimension for the analysis may differ. It also highlights how other analyses considering patterns of diversity change should carefully consider the rationale for accounting for spatial structure.

Despite the strong influence of spatial integrity on diversity estimation, this thesis also highlights the vital role of temporal continuity in estimating long-term diversity trends (**Chapter 4**). Longitudinal diversity monitoring can be interrupted for various reasons, generating data gaps in diversity records. If such cessations are accompanied by diversity change, the overall diversity trend estimation would be biased. In **Chapter 4,** I detect strong evidence that habitat change is associated with survey cessations in long-term diversity monitoring programmes. Habitat change is also associated with diversity loss in varying degrees (Jung *et al.*, 2019). Therefore, if this issue were not identified, this would result in a failure to properly detect diversity change governed by habitat alteration. Diversity trends estimated using longitudinal monitoring data may thus underestimate the diversity loss.

The interplay between people and nature

Human activity has been a major driver for global ecological change, shaping nature in different magnitudes, varieties and longevities (Lewis & Maslin, 2015). Human-induced changes, including land surface alteration and composition change of atmosphere, have led to critical diversity decline directly or indirectly (Barnosky *et al.*, 2011; Cardinale *et al.*, 2012; Pascual *et al.*, 2021). Therefore, anthropogenic impacts on multiple facets of diversity and conservation strategies to curb biodiversity loss have long been of significant interest in the field of ecology and conservation (Watson *et al.*, 2013; Waters *et al.*, 2016; Leclère *et al.*, 2020). However, change of nature influences human behaviours in turn (Cardinale *et al.*, 2012; Soga & Gaston, 2020). In such processes, how humans sense nature and what interactions can be obtained are the key prerequisites for responding to natural changes. These interactions, yet being profound for estimating diversity trends, have been relatively less studied (Gaston *et al.*, 2018).

Individual interactions with nature differ from each other (Gaston, 2020), suggesting that people's responses to environmental change and estimates of nature influenced by such responses can vary. Since observing nature can be the first and foremost step in diversity estimation, this suggests gaps between the actual and estimated nature and calls attention to likely biases underlying observations of different individuals. As discussed, I illustrate that survey behaviours in long-term biological survey programmes have different responses to habitat change (**Chapter 4**). I show that a significant proportion of the surveys tend to be ceased when there are habitat changes in the survey areas. As habitat change is often companied with diversity loss (Krauss *et al.*, 2010; Hautier *et al.*, 2015), such cessations

may lead to failures of recording declining diversity and bias the diversity trend estimation. Therefore, this chapter also implies the data limitation and potential bias in diversity estimation due to varying responses of people to natural environmental changes. Lack of considerations on such individual interactions may seriously inhibit the ability to accurately identify diversity trends across the planet.

One reflection of human interventions on nature is the conservation strategy in various forms that aim to stem biodiversity loss. Examples of such conservation interventions include prioritising global protected areas (Rodrigues *et al.*, 2004; Donaldson *et al.*, 2021), rewilding (Thévenin *et al.*, 2018; Perino *et al.*, 2019) and controlling invasive species (Roy *et al.*, 2014; Redding *et al.*, 2019). Yet determining future impacts of conservation interventions relies on the evidence-based performance in conservation (Sutherland *et al.*, 2004; Salafsky *et al.*, 2019). In **Chapter 5**, I tested whether one representative conservation strategy (i.e., rewilding) can effectively achieve its primary goal to fill native functional gaps. I show that rewilding mammals and birds in the UK did not contribute more functional uniqueness than other processes (e.g., unassisted colonisation, introduction) to the functional space of extant native assemblages. As reliable evidence of future performance and efficacy of interventions is a critical component of successful decision-making for environmental management (Sutherland *et al.*, 2004; Law *et al.*, 2017), this chapter implies that conservation translocation such as rewilding may need reassessment if infilling the functional gaps is a goal. This also highlights the complex ecology for direct conservation interventions and the evidence base to make accurate inferences.

Finally, I contribute to understanding how different species respond to human disturbance with two case studies. **Appendix E** shows that relatively more intensive human activities in farmlands in China are likely to cause China's wintering geese to use the farmland rarely. Migratory species' resilience to landscape changes also relies on spatial patterns of habitat degradation concerning their migratory movements (Gustafson & Parker, 1992; Xu *et al.*, 2014; Zhang *et al.*, 2018). **Appendix D** demonstrates that migratory geese with narrow migration corridors in the East Asian Flyways are more likely to be threatened by habitat degradation. Therefore, these findings provide insights on how anthropogenic impacts may shape biodiversity across species with distinct habitat requirements.

Future work

Assessing biodiversity patterns and trends in space and time is essential for conservation. Reliable biodiversity estimates, at multiple spatial scales (Chase *et al.*, 2019), allow us to track the global change progress to reduce the rate of biodiversity loss whilst allocating our limited conservation resources (Harrison *et al.*, 2014). In this thesis, I have surveyed the determinants of diversity estimation across spatial sampling coverages, scales and geographic structures, seeking insights from human behaviour, species response and their interactions.

Biodiversity synthesis

As anthropogenic impacts to Earth systems accelerate (Ceballos *et al.*, 2015), the past two decades have seen an explosion in the accessibility of global biodiversity information

describing the distribution, function, and evolutionary history of life on earth (Edwards *et al.*, 2000; Troudet *et al.*, 2018; Wüest *et al.*, 2020). It implies an urgent need for biodiversity knowledge integration to support responses to underpin a sustainable future (König *et al.*, 2019; Heberling *et al.*, 2021). This work highlights the potential biases underlying biodiversity datasets (**Chapter 4**), the effects of spatial coverage and scales on diversity estimates (**Chapter 2**), and the dynamic history that may influence the estimated diversity patterns (**Chapter 3**). Through these, attention could be called to different sampling strategies and histories to integrate disconnected datasets and build consolidated biodiversity data networks.

Incorporating both time and space dimensions

Scientists have long been interested in understanding the patterns, drivers, and consequences of biodiversity change both in certain locations and worldwide (Gaston, 2000; Barnosky *et al.*, 2011). However, these explorations sometimes fail to account for time and space dimensions together. Indeed, whilst the community history is essential for recognising diversity patterns (Chase, 2003), studies investigating the spatial heterogeneity of diversity distribution tended to focus on a static status across different areas, neglecting their dynamic diversity changes in the past (Devictor *et al.*, 2010; Morlon *et al.*, 2011; De Palma *et al.*, 2017). In **Chapter 3**, I illustrate that diversity distribution can be geographically neutral if considering the behaviour of diversity change in the past. This suggests that incorporating both time and space may resolve some controversial topics. For example, whether phylogenetic diversity can be a surrogate for the conservation of functional diversity is debated in the context of relatively static landscapes (Mazel *et al.*, 2018; Owen *et al.*, 2019),

and incorporating the continued diversity changes in the past may provide a novel direction to explore possible explanations.

Personalised ecology

The field of ecology has focused on understanding the relationship between species and the natural systems as free as possible from biases of human observations (Gaston *et al.*, 2018). However, it is seemingly unlikely to separate ecology studies from such biases, as interactions with nature are largely dependent on behaviour and opportunity at the level of individual people (Gaston, 2020). This requires attention to the biased ways in which different people encounter and interact with nature. From the perspective of diversity estimation, individual interactions with nature become increasingly crucial in estimating diversity changes. I show that survey behaviours may respond differently to habitat change in long-term diversity surveys (**Chapter 4**). Those varied survey behaviours may thus bias the diversity trend estimations, which also clue on different responses of individual surveyors to environmental change. As repositories of many types of data grow and theoretical frameworks develop, it will become feasible to account for individual influences on diversity estimates across scales. Unpacking these issues will constitute an exciting avenue of research and one that needs to be heavily informed in macroecology.

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Appendices

Appendix A

Supplementary material for
Chapter 3

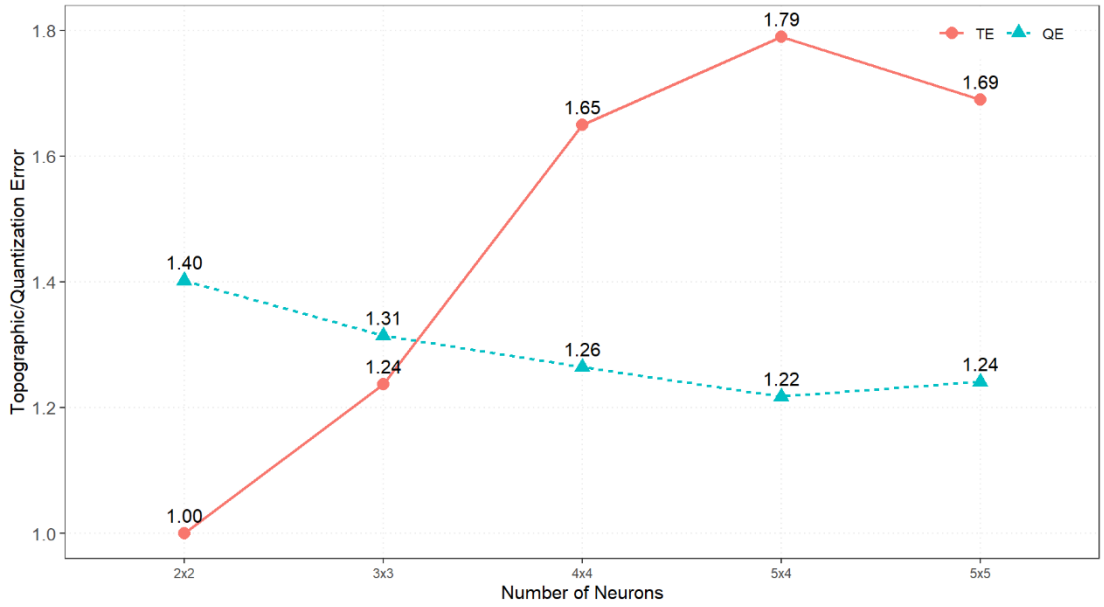

Figure S1. Topographic and quantization error changes with the number of neurons in the SOM for diversity time-series. The topographic error (TE) denotes the continuity of the mapping and the quantization error (QE) represents the average distance between each input time series and its neuron. Lower values of TE and QE indicate a smooth mapping, with similar time series mapped to close-by neurons

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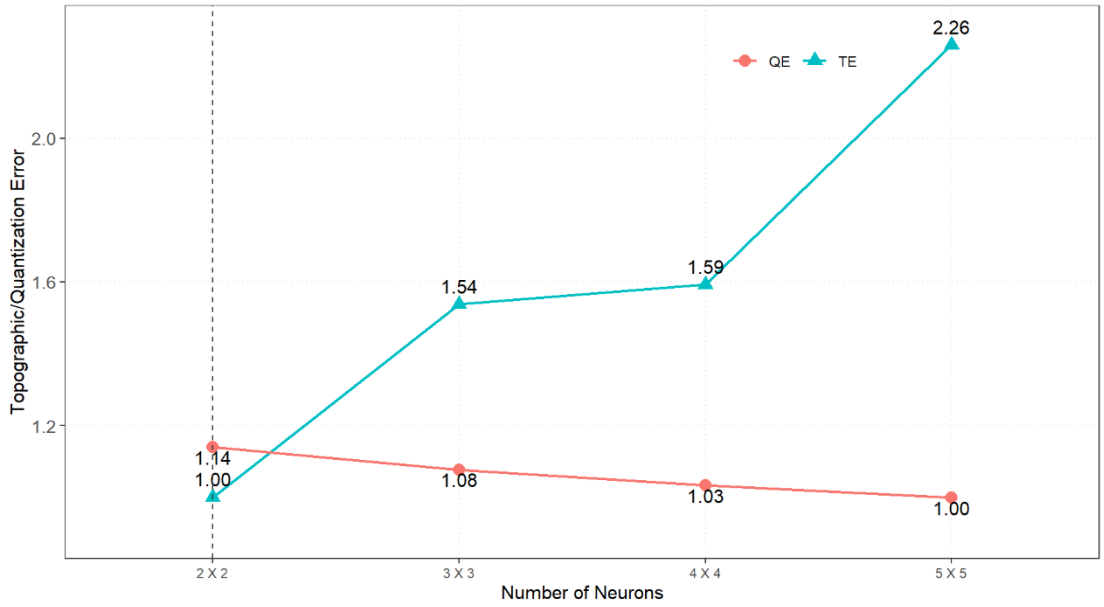

Figure S2. Topographic and quantization error changes with the number of neurons in the SOM for EVI time-series. The topographic error (TE) denotes the continuity of the mapping and the quantization error (QE) represents the average distance between each input time series and its neuron. Lower values of TE and QE indicate a smooth mapping, with similar time series mapped to close-by neurons.

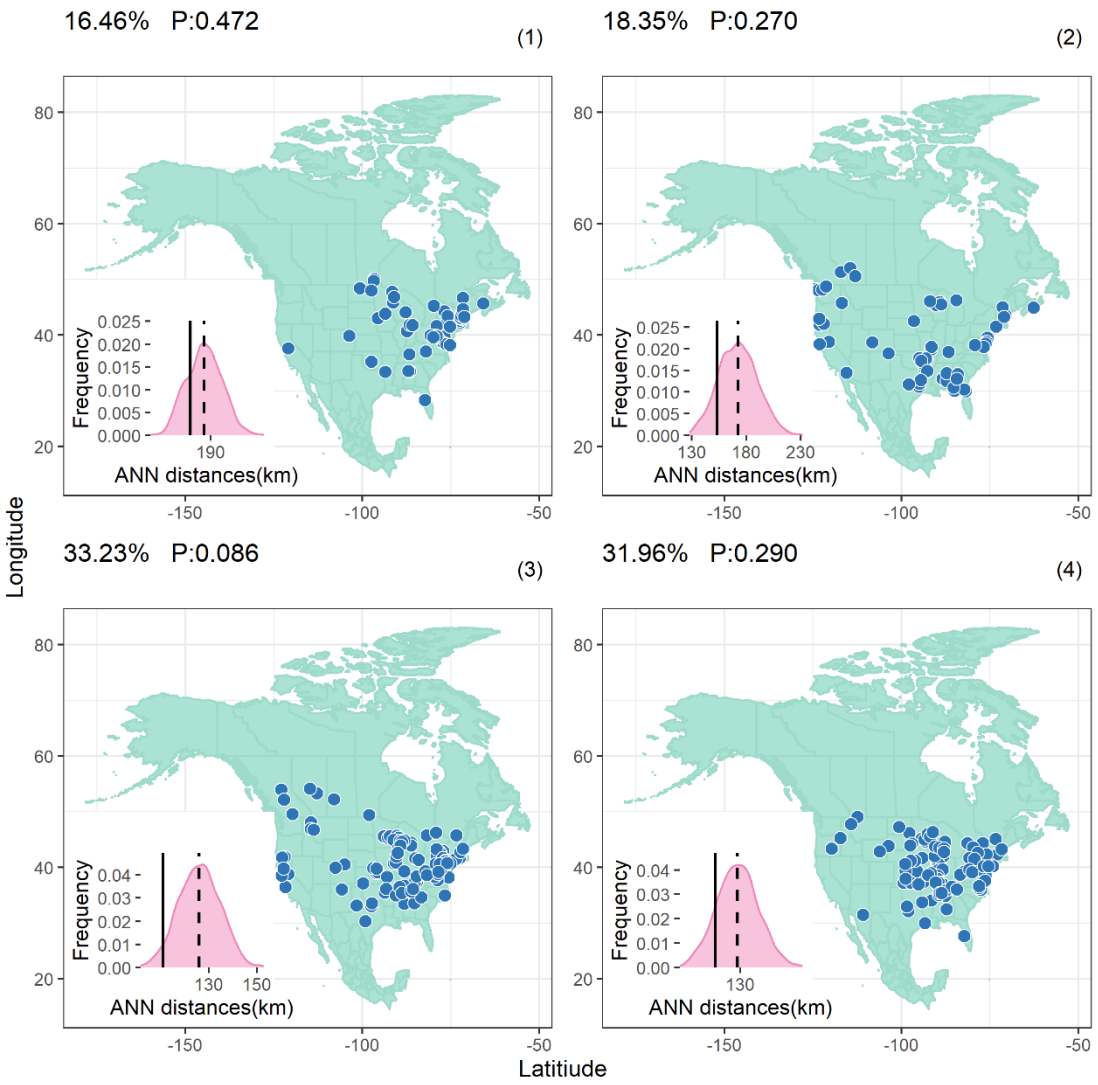

Figure S3. Spatial dependence test of route distribution within each pattern by a 2×2 self-organising map, with the solid line in the histogram showing the average nearest neighbour (ANN) distance of the survey routes and the density plot showing the distribution of ANN distance of 1000 Monte Carlo tests. A total number of 316 routes from 1973 -2016 were analysed. The blue points represent the start locations of each survey route. Percentages on the left top of each panel denote the percentages of time-series in that group to all time-series. Pseudo P-values represent the probability of incorrectness if rejecting the geographic independence hypothesis that diversity time-series that have the same pattern are randomly distributed.

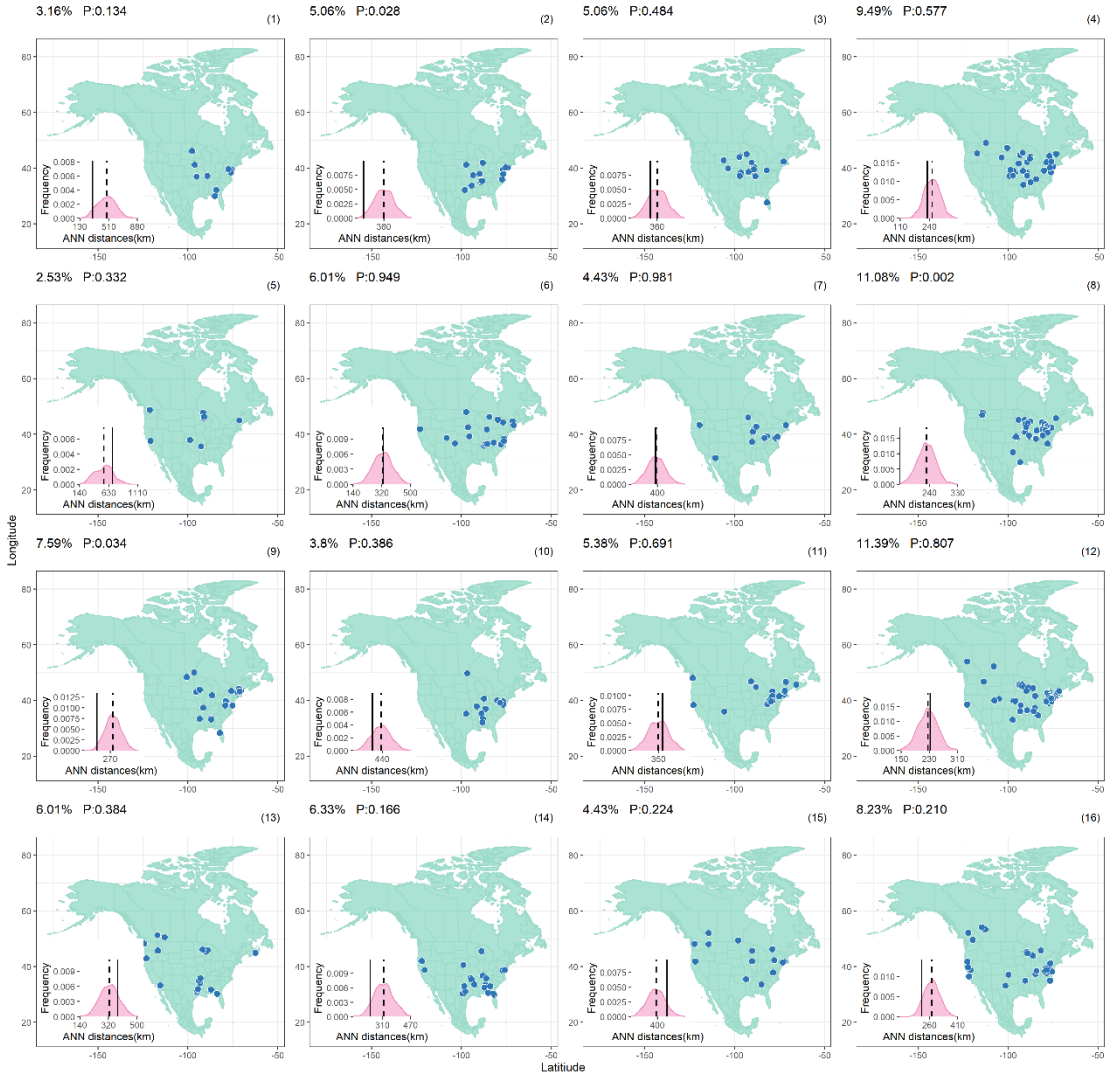

Figure S4. Spatial dependence test of route distribution within each pattern by a 4 × 4 self-organising map, with the solid line in the histogram showing the average nearest neighbour (ANN) distance of the survey routes and the density plot showing the distribution of ANN distance of 1000 Monte Carlo tests. A total number of 316 routes from 1973 -2016 were analysed. The blue points represent the start locations of each survey route. Percentages on the left top of each panel denote the percentages of time-series in that group to all time-series. Pseudo P-values represent the probability of incorrectness if rejecting the geographic independence hypothesis that diversity time-series that have the same pattern are randomly.

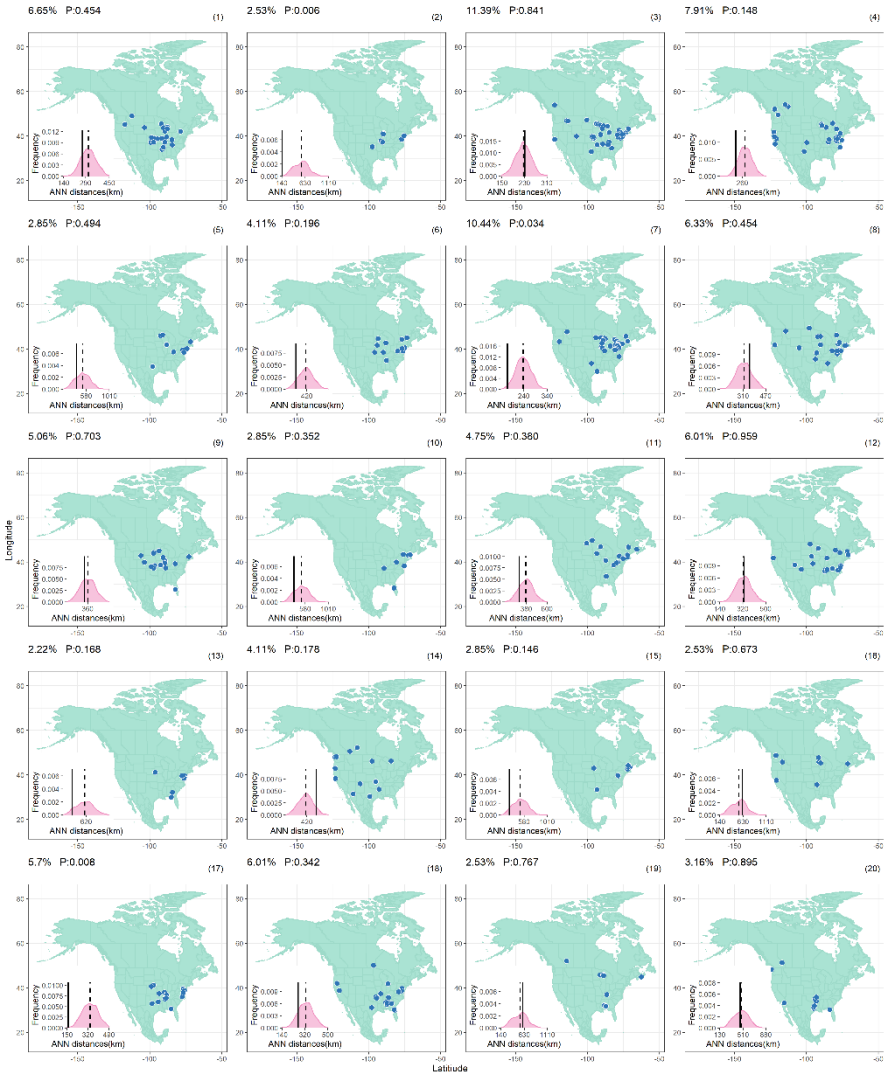

Figure S5. Spatial dependence test of route distribution within each pattern by a 5×4 self-organising map, with the solid line in the histogram showing the average nearest neighbour (ANN) distance of the survey routes and the density plot showing the distribution of ANN distance of 1000 Monte Carlo tests. A total number of 316 routes from 1973 -2016 were analysed. The blue points represent the start locations of each survey route. Percentages on the left top of each panel denote the percentages of time-series in that group to all time-series. Pseudo P-values represent the probability of incorrectness if rejecting the geographic independence hypothesis that diversity time-series that have the same pattern are randomly.

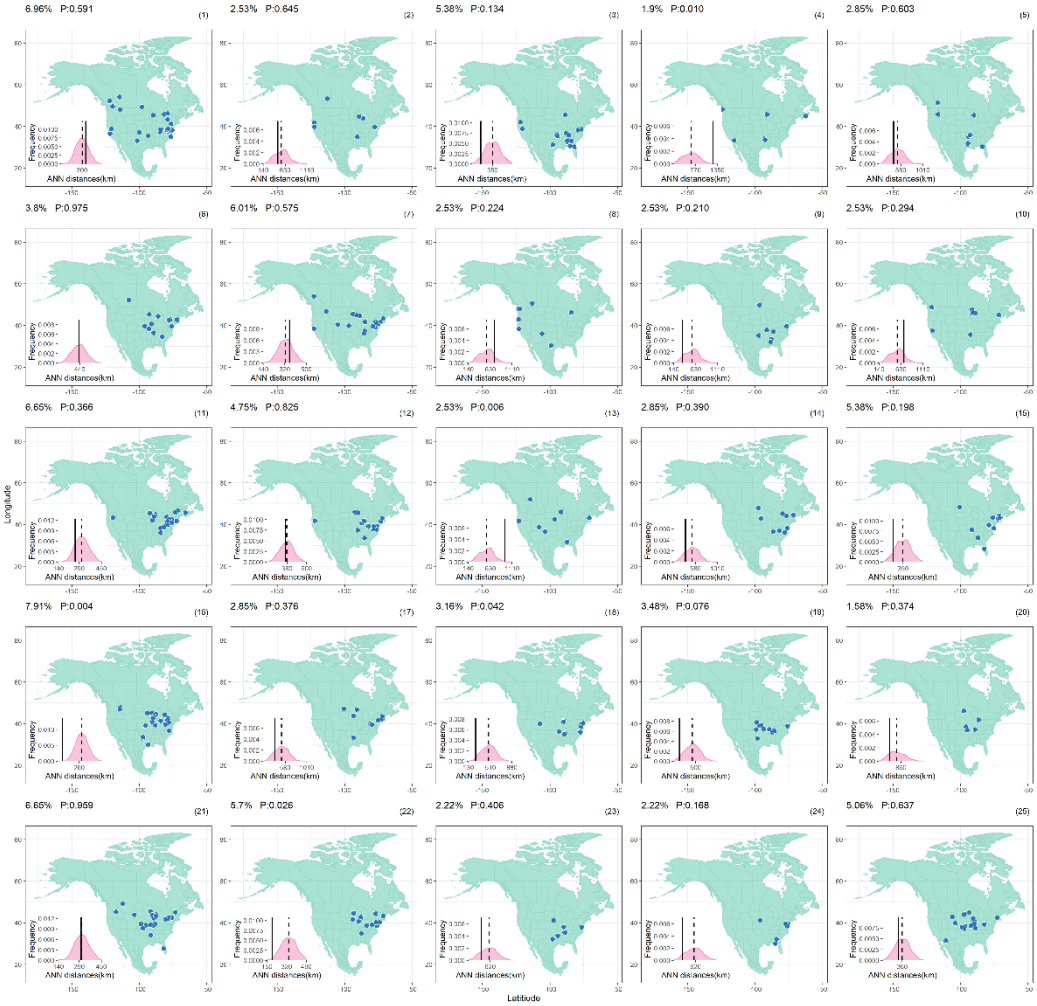

Figure S6. Spatial dependence test of route distribution within each pattern by a 5×5 self-organising map, with the solid line in the histogram showing the average nearest neighbour (ANN) distance of the survey routes and the density plot showing the distribution of ANN distance of 1000 Monte Carlo tests. A total number of 316 routes from 1973 -2016 were analysed. The blue points represent the start locations of each survey route. Percentages on the left top of each panel denote the percentages of time-series in that group to all time-series. Pseudo P-values represent the probability of incorrectness if rejecting the geographic independence hypothesis that diversity time-series that have the same pattern are randomly.



Figure S7. Temporal changes of taxonomic diversity, functional and phylogenetic diversity by a 2 × 2 self-organising map. The error bars represent 95% CI. The nonlinear regressions (a loess sliding window with a 33% range width; smoothed line) of the diversity facets were added to describe the major temporal trajectory at each pattern. Inner plots represent the correlation between diversity facets. FP is how FD changes with PD, FT is how FD changes with TD, and PT is how PD changes with TD.

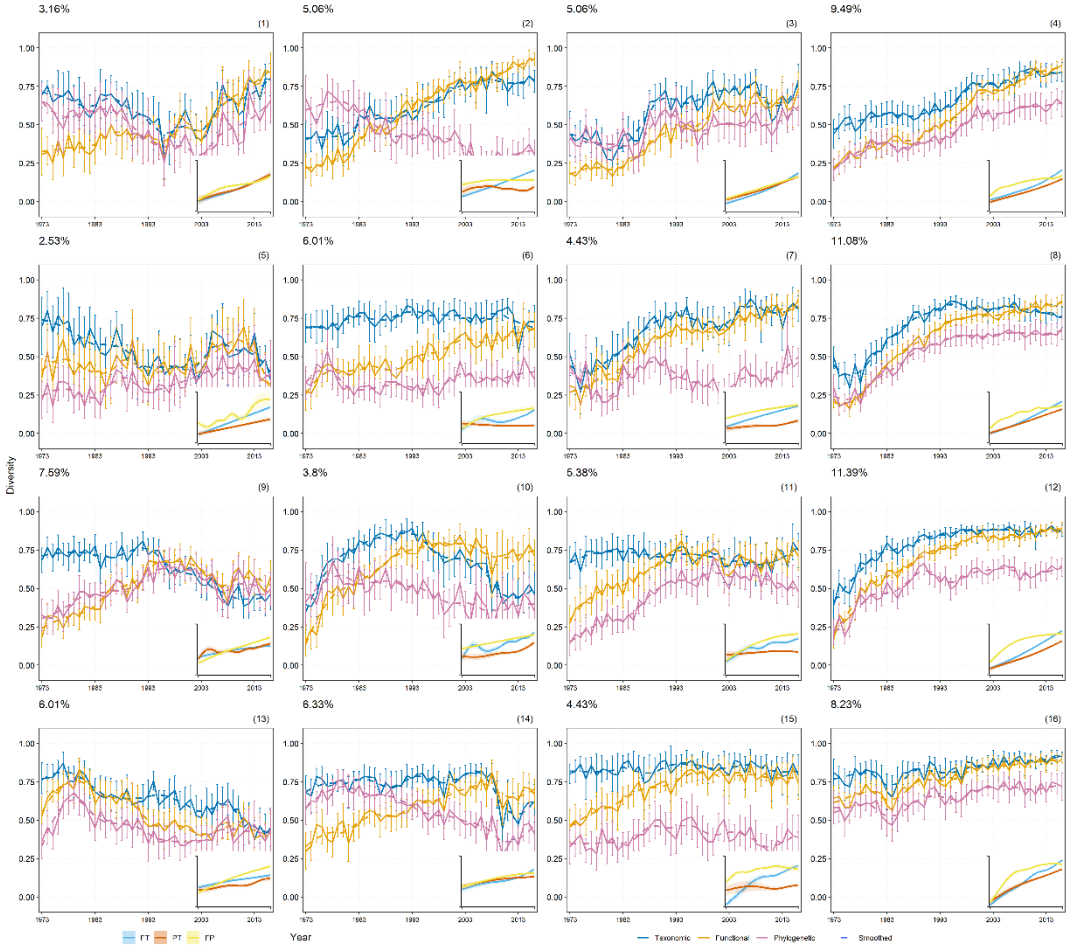

Figure S8. Temporal changes of taxonomic diversity, functional and phylogenetic diversity by a 4× 4 self-organising map. The error bars represent 95% CI. The nonlinear regressions (a loess sliding window with a 33% range width; smoothed line) of the diversity facets were added to describe the major temporal trajectory at each pattern. Inner plots represent the correlation between diversity facets. FP is how FD changes with PD, FT is how FD changes with TD, and PT is how PD changes with TD.

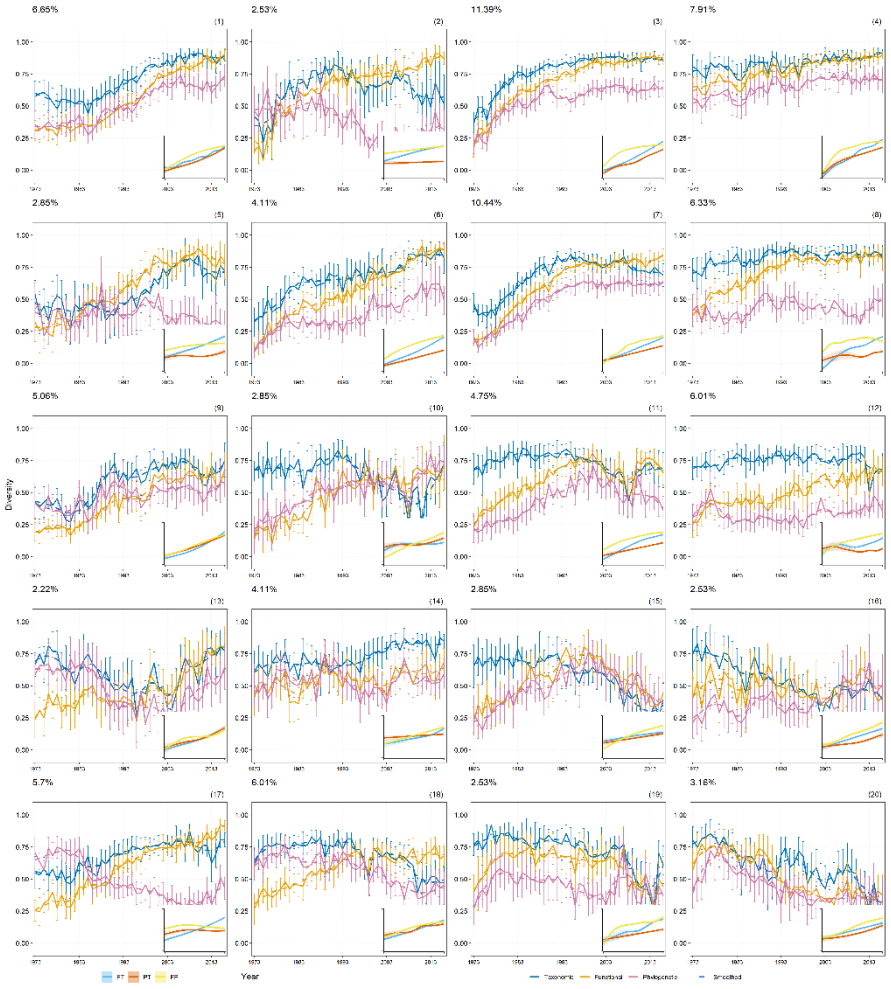

Figure S9. Temporal changes of taxonomic diversity, functional and phylogenetic diversity by a 5 × 4 self-organising map. The error bars represent 95% CI. The nonlinear regressions (a loess sliding window with a 33% range width; smoothed line) of the diversity facets were added to describe the major temporal trajectory at each pattern. Inner plots represent the correlation between diversity facets. FP is how FD changes with PD, FT is how FD changes with TD, and PT is how PD changes with TD.

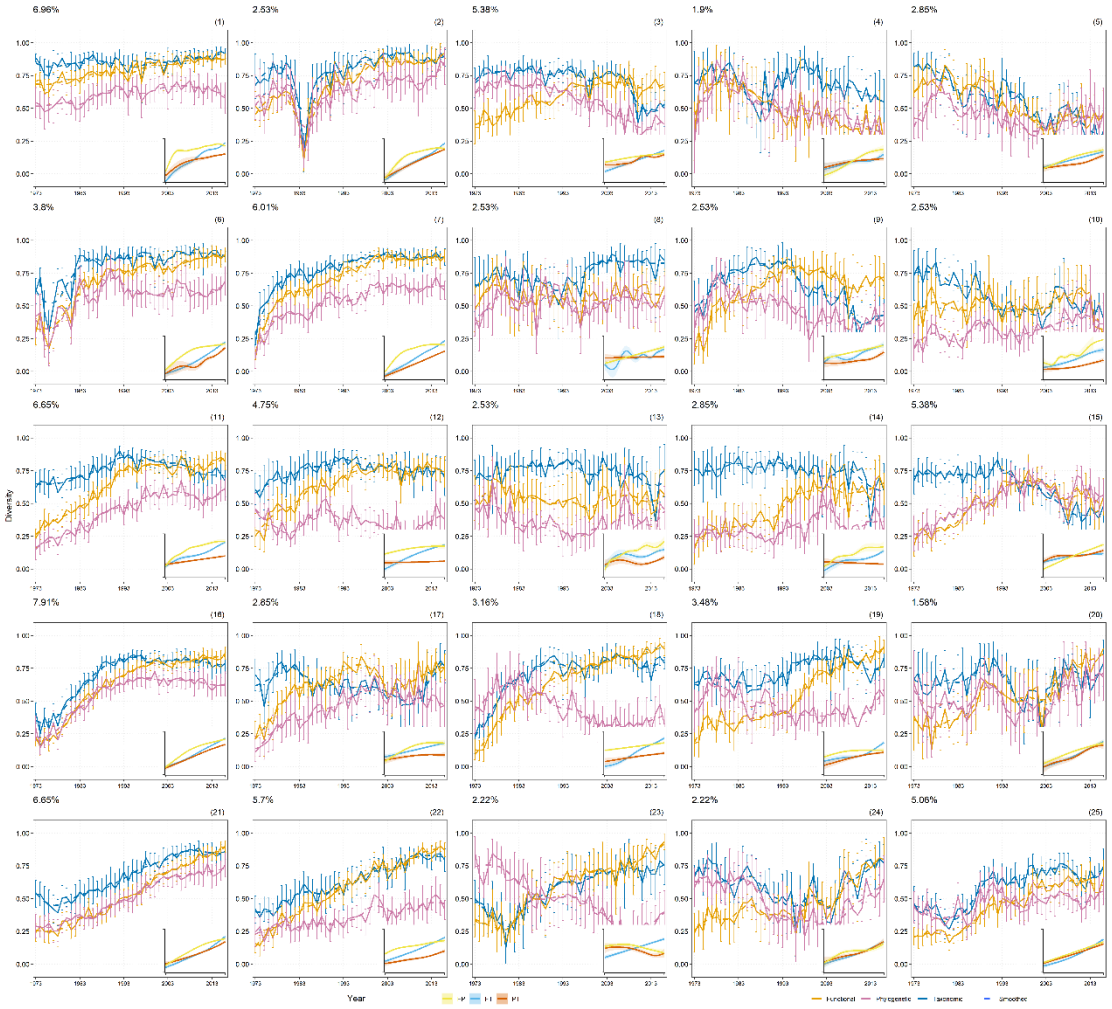

Figure S10. Temporal changes of taxonomic diversity, functional and phylogenetic diversity by a 5 × 5 self-organising map. The error bars represent 95% CI. The nonlinear regressions (a loess sliding window with a 33% range width; smoothed line) of the diversity facets were added to describe the major temporal trajectory at each pattern. Inner plots represent the correlation between diversity facets. FP is how FD changes with PD, FT is how FD changes

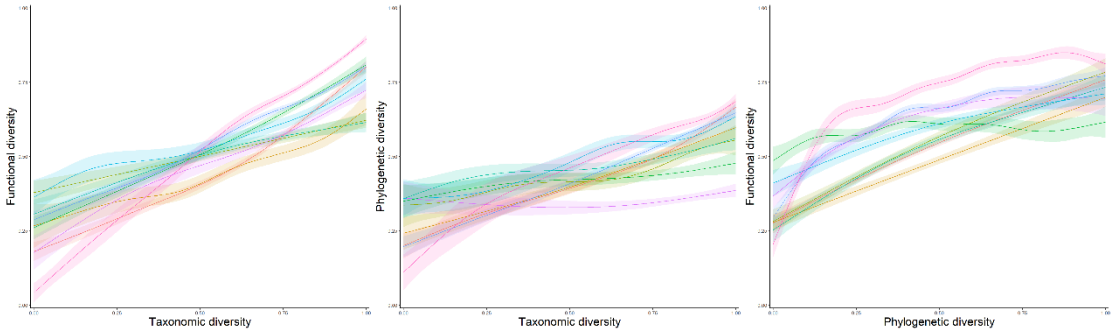

Figure S11. Correlation between taxonomic, functional, phylogenetic diversity for different groups of time-series in the North American Breeding Bird Survey for a 3 × 3 self-organising map. Relationship was measured by generalised additive model (GAM). The error bars represent 95% CI. Different colours represent different groups of diversity time-series.

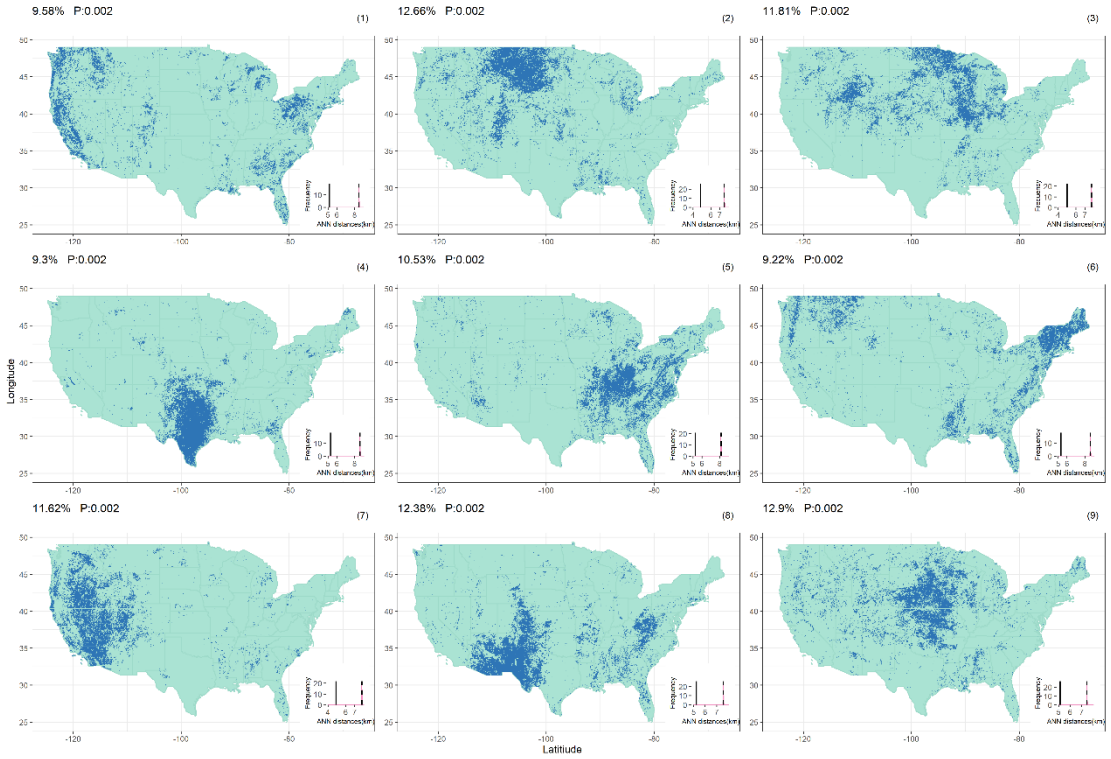

Figure S12. Distribution of enhanced vegetation index (EVI) time-series in full coverage of the contiguous United States and spatial independence test by a 3×3 self-organising map. Each panel presents the distribution of EVI time-series (blue pixels) that have the same pattern. The inset density plot shows the distribution of ANN distance of 1000 Monte Carlo tests. The solid lines in the density plot represent the average nearest neighbour (ANN) distance of the locations of EVI time-series and dashed lines represent the mean value of ANN for 1000 random samples. Percentages on the left top of each panel denote the percentages of time-series in that group to all time-series. Pseudo P-values represent the probability of incorrectness if rejecting the geographic independence hypothesis that EVI time-series that have the same pattern are randomly distributed.

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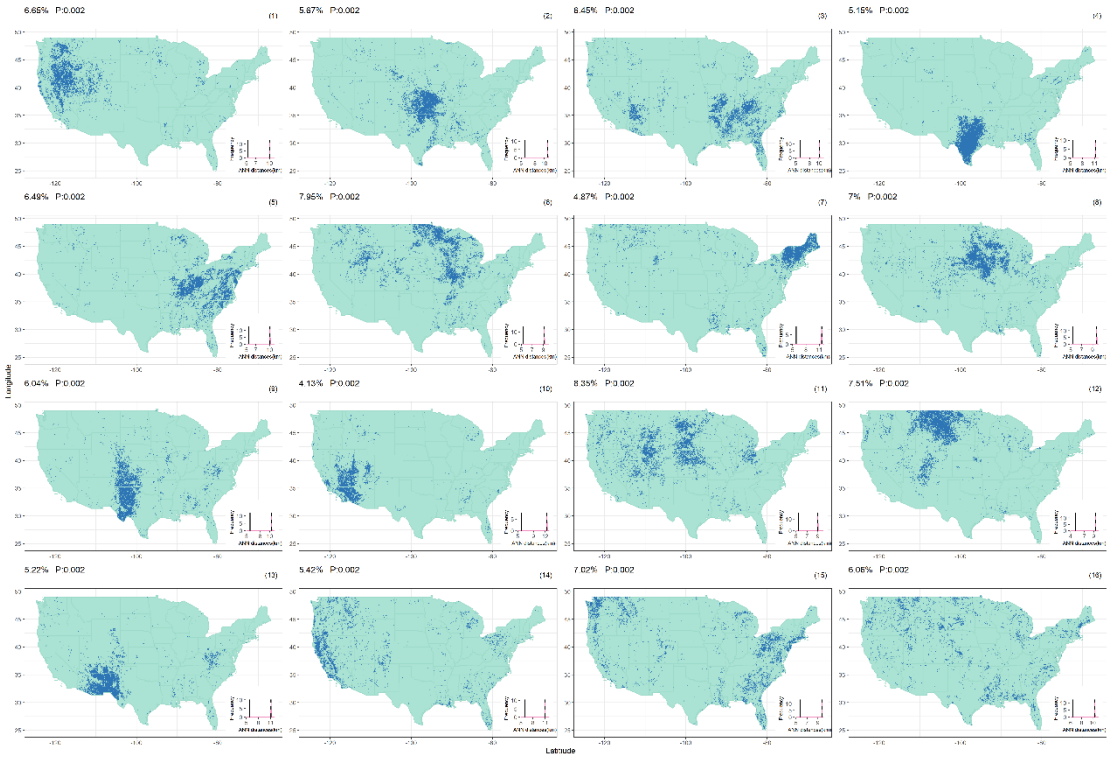

Figure S13. Distribution of enhanced vegetation index (EVI) time-series in full coverage of the contiguous United States and spatial independence test by a 4×4 self-organising map. Each panel presents the distribution of EVI time-series (blue pixels) that have the same pattern. The inset density plot shows the distribution of ANN distance of 1000 Monte Carlo tests. The solid lines in the density plot represent the average nearest neighbour (ANN) distance of the locations of EVI time-series and dashed lines represent the mean value of ANN for 1000 random samples. Percentages on the left top of each panel denote the percentages of time-series in that group to all time-series. Pseudo P-values represent the probability of incorrectness if rejecting the geographic independence hypothesis that EVI time-series that have the same pattern are randomly distributed.

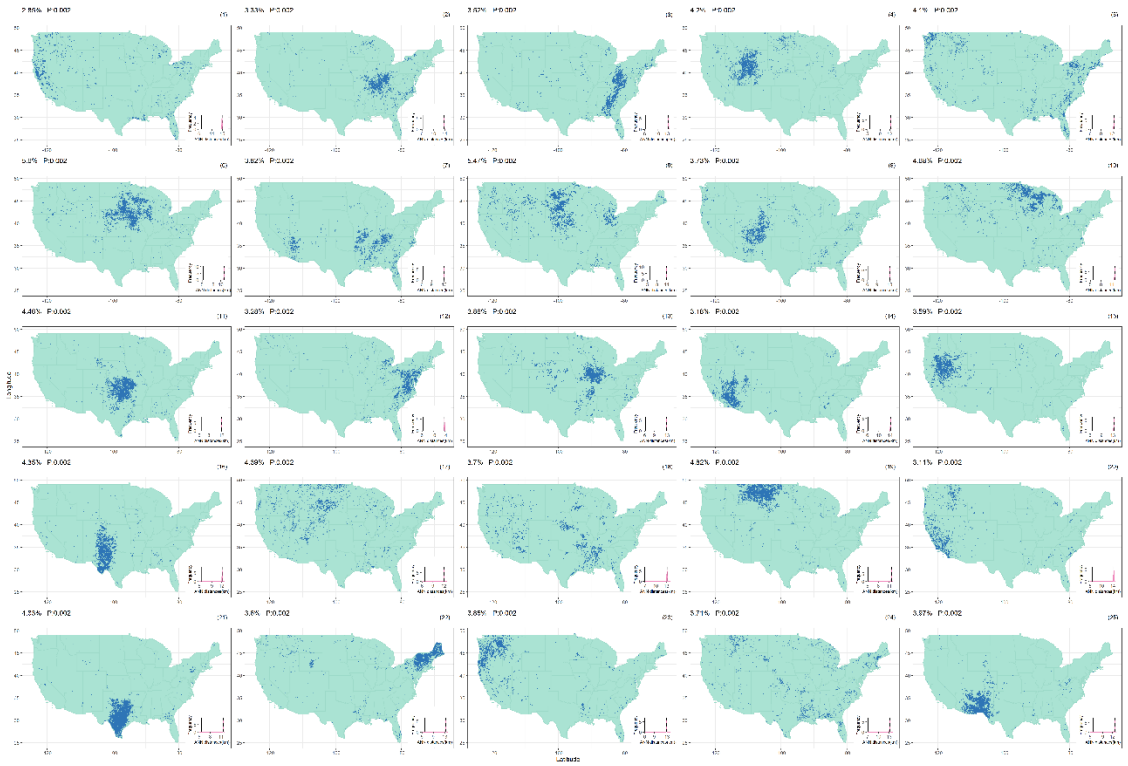

Figure S14. Distribution of enhanced vegetation index (EVI) time-series in full coverage of the contiguous United States and spatial independence test by a 5×5 self-organising map. Each panel presents the distribution of EVI time-series (blue pixels) that have the same pattern. The inset density plot shows the distribution of ANN distance of 1000 Monte Carlo tests. The solid lines in the density plot represent the average nearest neighbour (ANN) distance of the locations of EVI time-series and dashed lines represent the mean value of ANN for 1000 random samples. Percentages on the left top of each panel denote the percentages of time-series in that group to all time-series. Pseudo P-values represent the probability of incorrectness if rejecting the geographic independence hypothesis that EVI time-series that have the same pattern are randomly distributed.

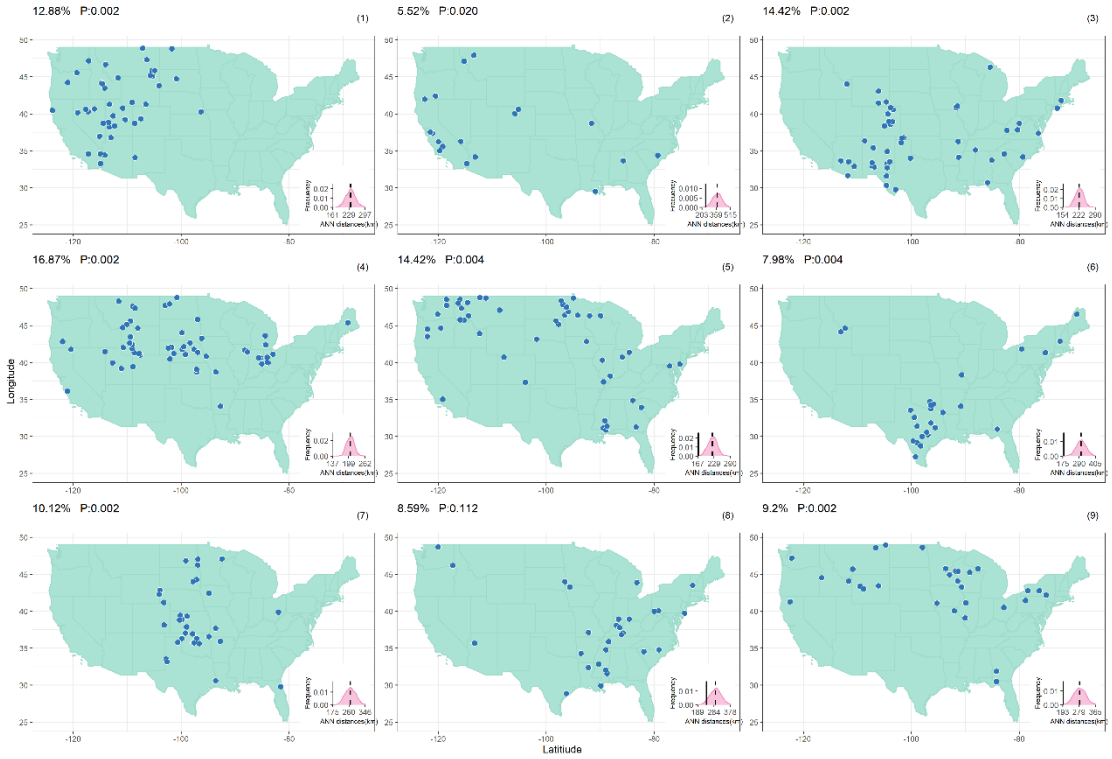

Figure S15. Distribution of enhanced vegetation index (EVI) time-series in 0.1% sample coverage of the contiguous United States and spatial independence test by a 3×3 self-organising map. Each panel presents the distribution of EVI time-series (blue pixels) that have the same pattern. The inset density plot shows the distribution of ANN distance of 1000 Monte Carlo tests. The solid lines in the density plot represent the average nearest neighbour (ANN) distance of the locations of EVI time-series and dashed lines represent the mean value of ANN for 1000 random samples. Percentages on the left top of each panel denote the percentages of time-series in that group to all time-series. Pseudo P-values represent the probability of incorrectness if rejecting the geographic independence hypothesis that EVI time-series that have the same pattern are randomly distributed.

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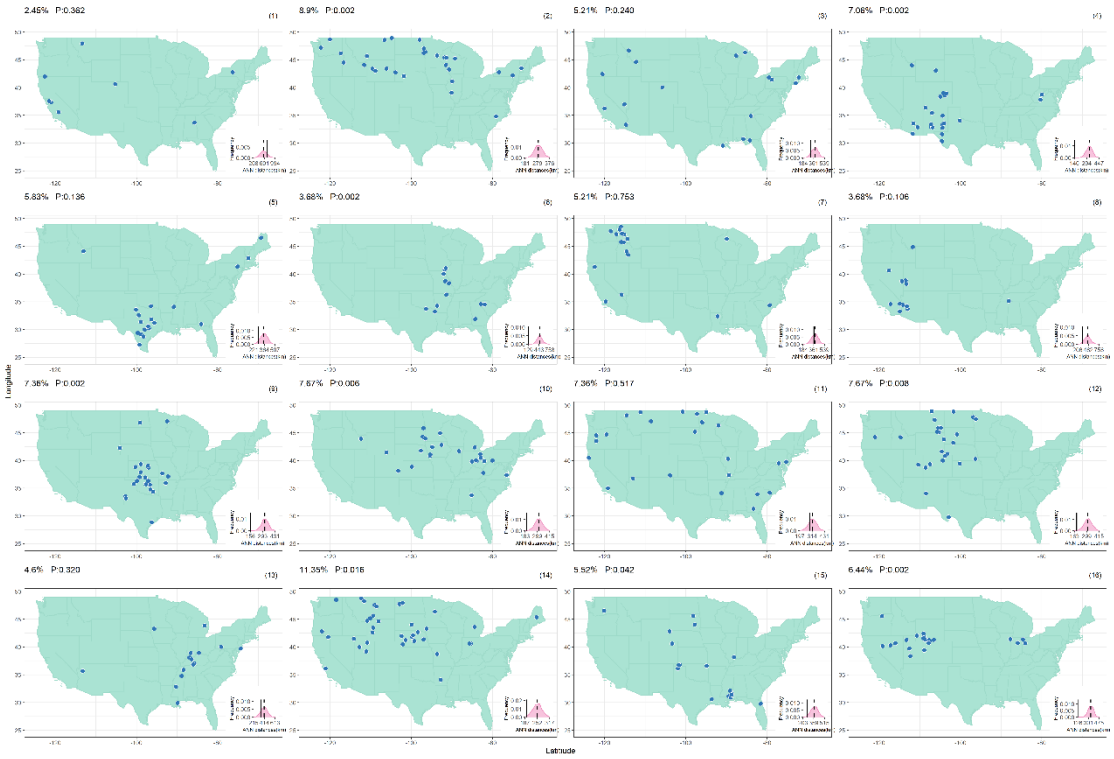

Figure S16. Distribution of enhanced vegetation index (EVI) time-series in 0.1% sample coverage of the contiguous United States and spatial independence test by a 4×4 self-organising map. Each panel presents the distribution of EVI time-series (blue pixels) that have the same pattern. The inset density plot shows the distribution of ANN distance of 1000 Monte Carlo tests. The solid lines in the density plot represent the average nearest neighbour (ANN) distance of the locations of EVI time-series and dashed lines represent the mean value of ANN for 1000 random samples. Percentages on the left top of each panel denote the percentages of time-series in that group to all time-series. Pseudo P-values represent the probability of incorrectness if rejecting the geographic independence hypothesis that EVI time-series that have the same pattern are randomly distributed.



Figure S17. Distribution of enhanced vegetation index (EVI) time-series in 0.1% sample coverage of the contiguous United States and spatial independence test by a 5×5 self-organising map. Each panel presents the distribution of EVI time-series (blue pixels) that have the same pattern. The inset density plot shows the distribution of ANN distance of 1000 Monte Carlo tests. The solid lines in the density plot represent the average nearest neighbour (ANN) distance of the locations of EVI time-series and dashed lines represent the mean value of ANN for 1000 random samples. Percentages on the left top of each panel denote the percentages of time-series in that group to all time-series. Pseudo P-values represent the probability of incorrectness if rejecting the geographic independence hypothesis that EVI time-series that have the same pattern are randomly distributed.

Appendix B

Supplementary material for
Chapter 4

Habitat change and biased sampling influence estimation of diversity trends

Highlights

- Longitudinal bird-monitoring surveys are more likely to cease when habitat changes
- Major habitat changes affect biodiversity trends
- Biodiversity loss can therefore be underestimated due to sampling bias over time

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In brief

Zhang et al. demonstrate that data gaps in longitudinal bird surveys are often associated with habitat changes. While habitat changes affect biodiversity trends, they can lead to failure to record biodiversity loss, which ultimately causes under-reporting of biodiversity loss from time series data and under-representing of impacts of habitat change.

Supplemental Information

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https://doi.org/10.1016/j.cub.2021.05.066

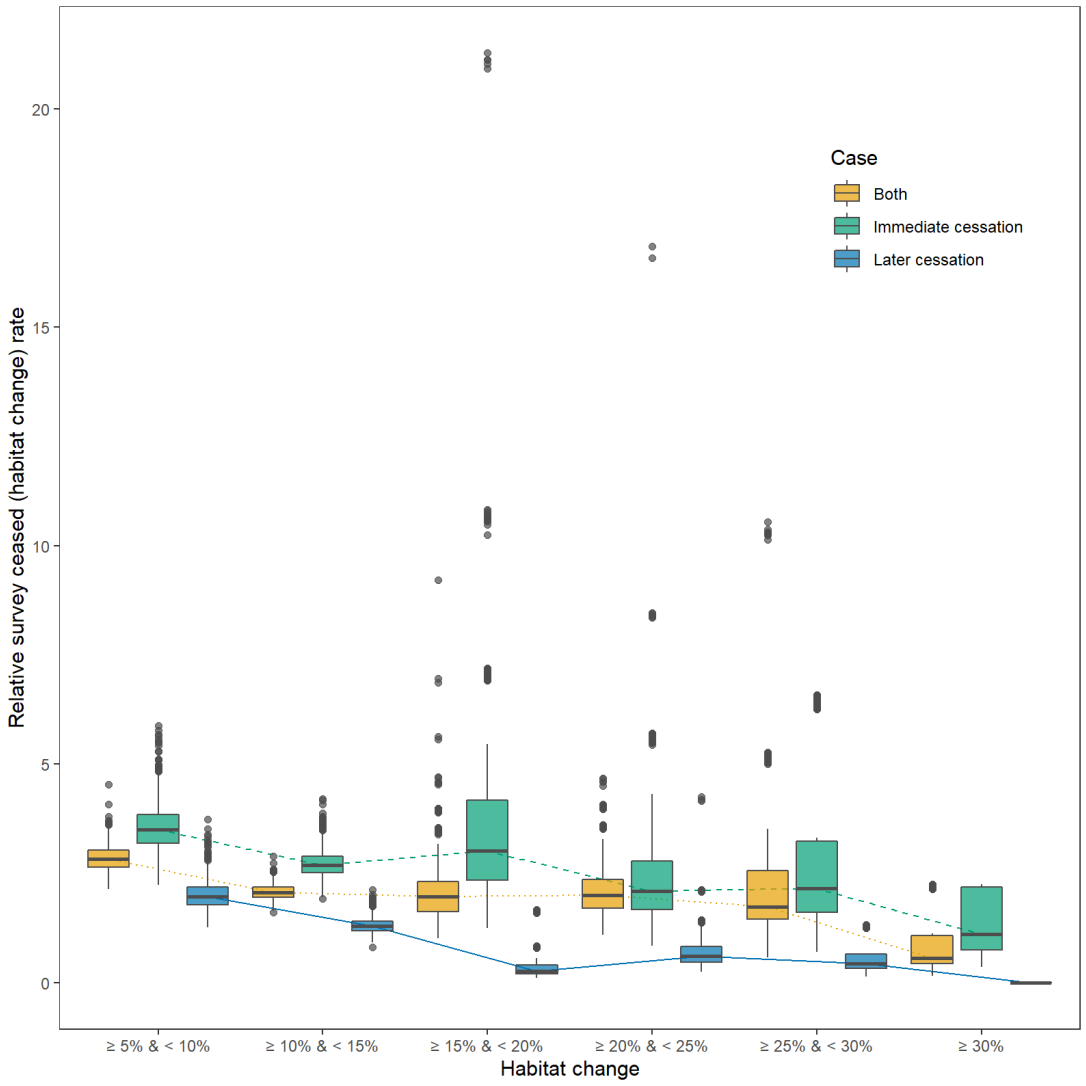

Figure S1. Change of the relative survey ceased (habitat change) rates in both immediate and later survey cessation routes for habitat changes of multiple categories. Related to Figure 2. The relative survey ceased (habitat change) rate for a given proportion of habitat change (k) is calculated by $RR_{HCS,k} = \frac{sR_{HCS,k}}{rR_{HCS,k}}$, where sR_k is the actual proportion of routes with habitat change above k where surveying was ceased, and rR_k is the proportion of routes with randomly distributed habitat change above k where surveying was ceased. The randomised procedure was replicated 1000 times. Boxes represent the 25th and 75th percentiles, lines within the boxes represent the 50th percentile (median), and whiskers represent 2.5th and 97.5th

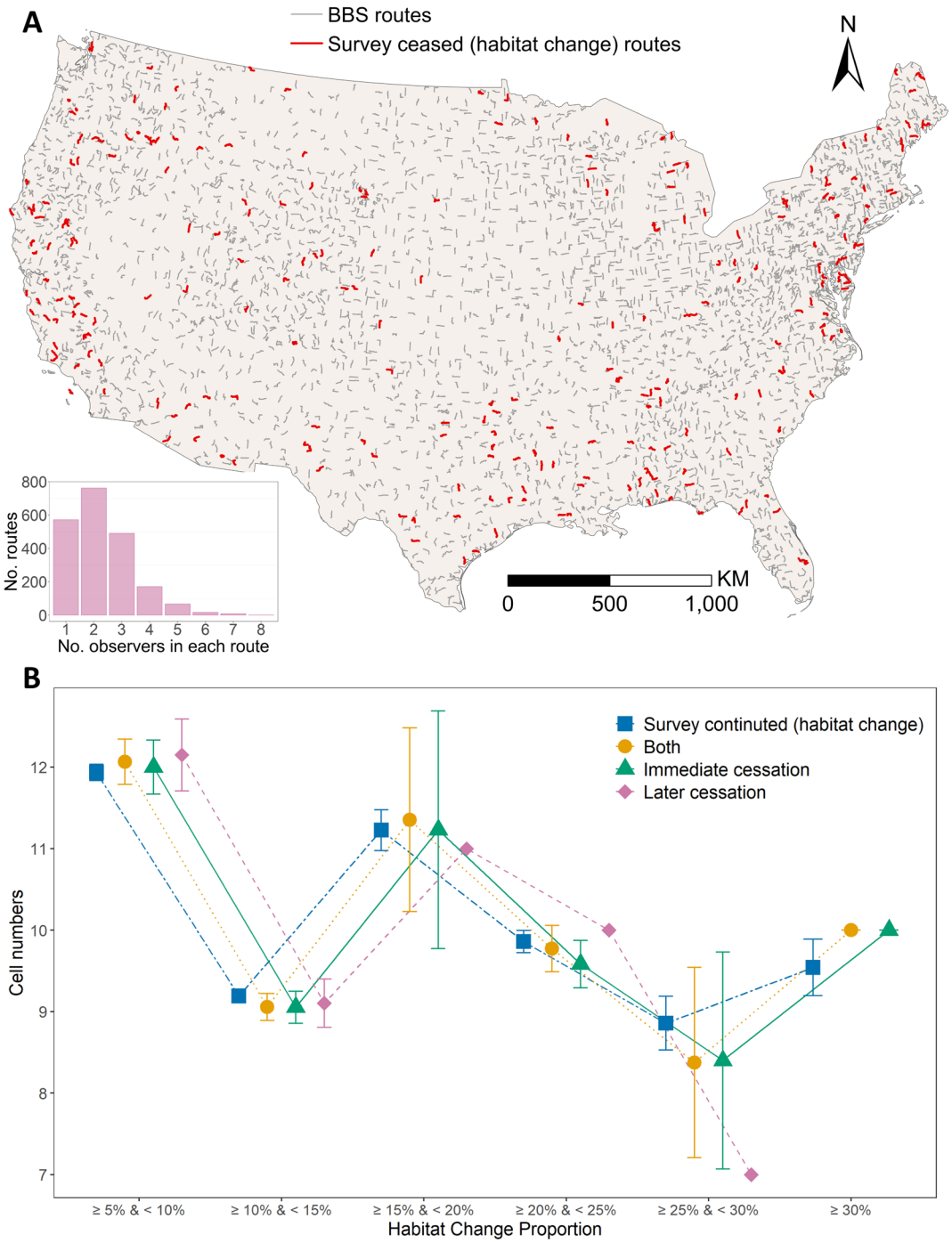

Figure S2. The distribution and summary of the survey routes in North American Breeding Survey programme. Related to Figure 2 and STAR Methods. A. BBS routes are the whole 3014 routes and survey ceased (habitat change) routes are the routes of habitat change over 5% around their neighbourhood and associated with survey cessations. The inset plot denotes the number of routes with different numbers of observers. **B.** Area of the neighbourhood around each route in different habitat change proportion presented by cell numbers extracted from the land cover map within 5-km buffer**.** The points represent the mean value of the relative diversity change and error bars represents 95% CI.

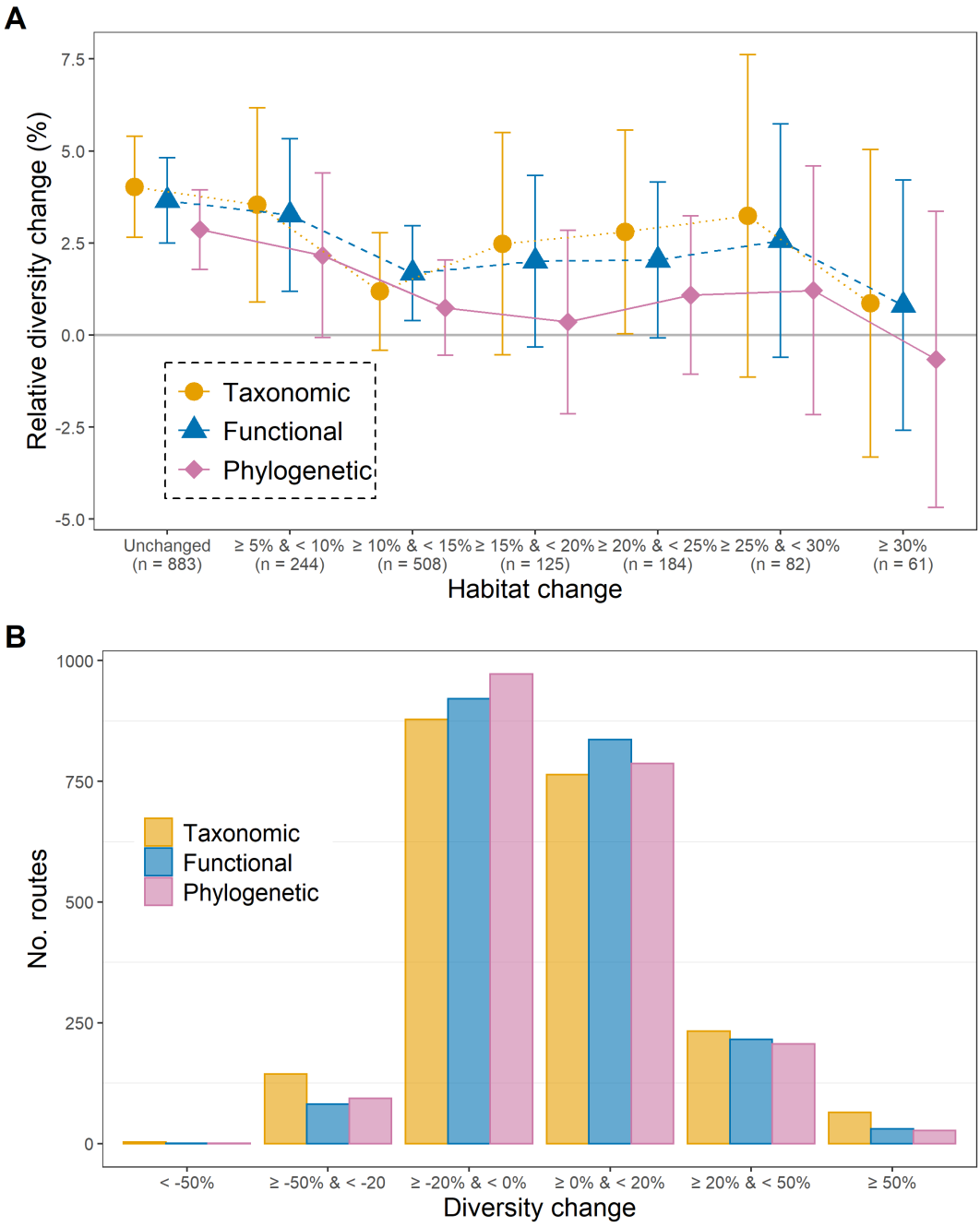

Figure S3. Diversity changes. Related to Figure 3. A. Relative diversity changes between 2001-2003 and 2016-2018 for routes without habitat change and routes with habitat change estimated at 5% - 10%, 10% - 15%, 15% - 20%, 20% - 25%, 25% - 30% and more than 30%. The points represent the mean value of the relative diversity change and error bars represents 95% CI. **B.** Number of survey continued routes with relative diversity change at less than -50%, -50% - -20%, -20% - 0%, 0% - 20%, 20% - 50% and more than 50%. Different colours denote different diversity forms.

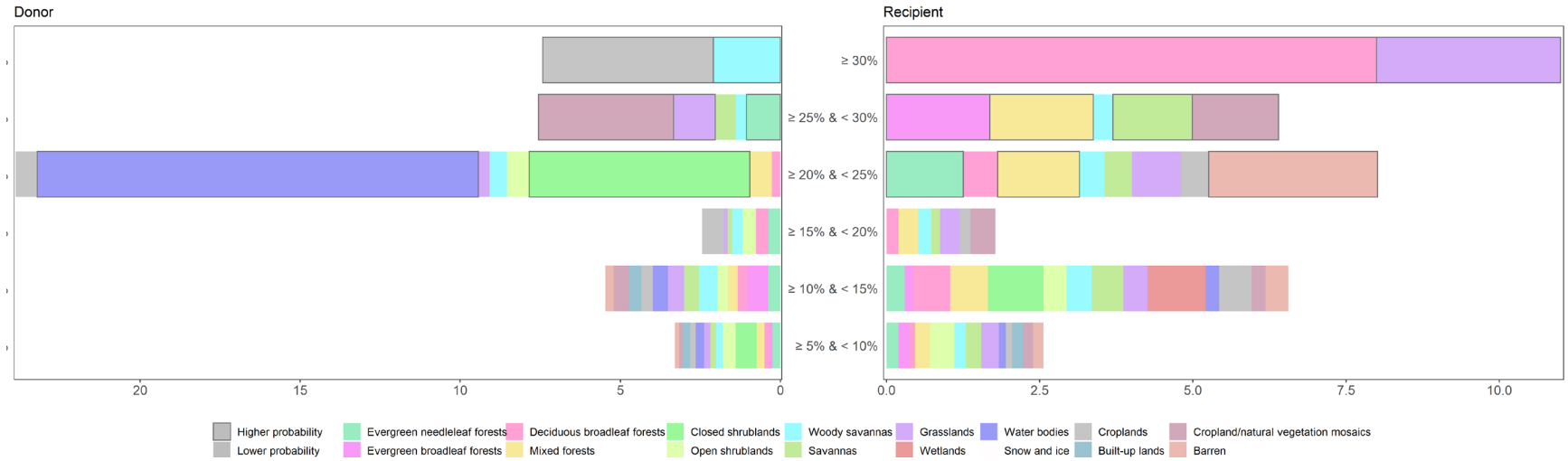

Figure S4. Proportions of habitat change types. Related to Figure 3. Donor means habitat loss and recipient means habitat increase. The bar denotes probability for a given a habitat type that likely caused survey cessation for a given habitat change proportion k, calculated by $CP_{i,k} = \frac{n_{i,k}/n_k}{N_{i,k}/N_k}$, where $CP_{i,k}$ is the ceased probability for a donor or recipient habitat type i, $n_{i,k}$ is the number of survey ceased (habitat change) routes by habitat type i, n_k is the total number of survey ceased (habitat change) routes, $N_{i,k}$ is the number of routes with habitat change in habitat type i, and N_k is the total number of routes with habitat change. $CP_{i,k}$ approaches 0 for minimum probability and increases more than 1 for higher probability. Different colours represent different habitat types.

Appendix C

Supplementary material for
Chapter 5

Table S1. Category of birds in the UK.

English	Scientific	Natural	Anthropogenic	Reference 1	Reference 2	Reference 3	Reference 4	Reference 5
Eurasian Golden Oriole	*Oriolus oriolus*	Extirpated	Extirpated	Yalden, Derek, and Umberto Albarella. The History of British Birds. Oxford University Press, 2009.				
Eurasian Wryneck	*Jynx torquilla*	Extirpated	Extirpated	Yalden, Derek, and Umberto Albarella. The History of British Birds. Oxford University Press, 2009.				
Kentish Plover	*Charadrius alexandrinus*	Extirpated	Extirpated	Yalden, Derek, and Umberto Albarella. The History of British Birds. Oxford University Press, 2009.				
Red-backed Shrike	*Lanius collurio*	Extirpated	Extirpated	Yalden, Derek, and Umberto Albarella. The History of British Birds. Oxford University Press, 2009.				
Temminck's Stint	*Calidris temminckii*	Extirpated	Extirpated	Yalden, Derek, and Umberto Albarella. The History of British Birds. Oxford University Press, 2009.				
Alexandrine Parakeet	*Psittacula eupatria*	Introduced	Introduced	McInerny, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.				
Atlantic Canary	*Serinus canaria*	Introduced	Introduced	McInerny, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.				
Bar-headed Goose	*Anser indicus*	Introduced	Introduced	McInerny, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.				
Black Swan	*Cygnus atratus*	Introduced	Introduced	McInerny, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.				
Blue-crowned Parakeet	*Aratinga acuticaudata*	Introduced	Introduced	McInerny, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.				
Budgerigar	*Melopsittacus undulatus*	Introduced	Introduced	McInerny, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.				
Chukar Partridge	*Alectoris chukar*	Introduced	Introduced	McInerny, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.				
Cinnamon Teal	*Anas cyanoptera*	Introduced	Introduced	McInerny, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.				
Emperor Goose	*Chen canagica*	Introduced	Introduced	McInerny, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.				
Eurasian Eagle-Owl	*Bubo bubo*	Introduced	Introduced	McInerny, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.				
Harris's Hawk	*Parabuteo unicinctus*	Introduced	Introduced	McInerny, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.				
Helmeted Guineafowl	*Numida meleagris*	Introduced	Introduced	McInerny, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.				
Indian Peafowl	*Pavo cristatus*	Introduced	Introduced	McInerny, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.				
Lady Amherst's Pheasant	*Chrysolophus amherstiae*	Introduced	Introduced	McInerny, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.				
Monk Parakeet	*Myiopsitta monachus*	Introduced	Introduced	McInerny, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.				

Muscovy Duck	*Cairina moschata*	Introduced	Introduced	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
Reeves's Pheasant	*Syrmaticus reevesii*	Introduced	Introduced	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
Ross's Goose	*Chen rossii*	Introduced	Introduced	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
Rosy-faced Lovebird	*Agapornis roseicollis*	Introduced	Introduced	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
Silver Pheasant	*Lophura nycthemera*	Introduced	Introduced	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
South African Shelduck	*Tadorna cana*	Introduced	Introduced	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
Swan Goose	*Anser cygnoides*	Introduced	Introduced	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
Trumpeter Swan	*Cygnus buccinator*	Introduced	Introduced	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
Upland Goose	*Chloephaga picta*	Introduced	Introduced	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
Wild Turkey	*Meleagris gallopavo*	Introduced	Introduced	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
Wood Duck	*Aix sponsa*	Introduced	Introduced	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com
Arctic Tern	*Sterna paradisaea*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com
Atlantic Puffin	*Fratercula arctica*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com
Barn Swallow	*Hirundo rustica*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com
Bearded Tit	*Panurus biarmicus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
Bittern	*Botaurus stellaris*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com
Black Grouse	*Tetrao tetrix*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
Black Guillemot	*Cepphus grylle*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com
Black Redstart	*Phoenicurus ochruros*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com
Blackbird	*Turdus merula*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com
Blackcap	*Sylvia atricapilla*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com

Black-headed Gull	*Larus ridibundus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Black-legged Kittiwake	*Rissa tridactyla*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Black-necked Grebe	*Podiceps nigricollis*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Black-throated Diver	*Gavia arctica*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Blue Tit	*Parus caeruleus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Carrion Crow	*Corvus corone*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Chaffinch	*Fringilla coelebs*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Coal Tit	*Parus ater*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Buzzard	*Buteo buteo*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Chiffchaff	*Phylloscopus collybita*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Cuckoo	*Cuculus canorus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Eider	*Somateria mollissima*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Goldeneye	*Bucephala clangula*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Greenshank	*Tringa nebularia*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Guillemot	*Uria aalge*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Kestrel	*Falco tinnunculus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Kingfisher	*Alcedo atthis*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Merganser	*Mergus merganser*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Moorhen	*Gallinula chloropus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Nightingale	*Luscinia megarhynchos*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Pochard	*Aythya ferina*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.

Common Quail	*Coturnix coturnix*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Redpoll	*Carduelis flammea*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Redshank	*Tringa totanus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Redstart	*Phoenicurus phoenicurus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Ringed Plover	*Charadrius hiaticula*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Sandpiper	*Actitis hypoleucos*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Scoter	*Melanitta nigra*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Shelduck	*Tadorna tadorna*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Snipe	*Gallinago gallinago*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Starling	*Sturnus vulgaris*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Swift	*Apus apus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Tern	*Sterna hirundo*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Common Whitethroat	*Sylvia communis*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Coot	*Fulica atra*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Corn Bunting	*Miliaria calandra*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Crested Tit	*Parus cristatus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
Dartford Warbler	*Sylvia undata*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
Dunlin	*Calidris alpina*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Dunnock	*Prunella modularis*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Eurasian Bullfinch	*Pyrrhula pyrrhula*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Eurasian Curlew	*Numenius arquata*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.

Eurasian Dotterel	*Eudromias morinellus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Eurasian Hobby	*Falco subbuteo*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Eurasian Jay	*Garrulus glandarius*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Eurasian Oystercatcher	*Haematopus ostralegus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Eurasian Siskin	*Carduelis spinus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Eurasian Skylark	*Alauda arvensis*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Eurasian Sparrowhawk	*Accipiter nisus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Eurasian Teal	*Anas flavirostris*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Eurasian Tree Sparrow	*Passer montanus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Eurasian Treecreeper	*Certhia familiaris*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Eurasian Wigeon	*Anas penelope*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Eurasian Woodcock	*Scolopax rusticola*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
European Goldfinch	*Carduelis carduelis*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
European Greenfinch	*Carduelis chloris*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
European Pied Flycatche	*Ficedula hypoleuca*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
European Robin	*Erithacus rubecula*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
European Shag	*Phalacrocorax aristotelis*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Garden Warbler	*Sylvia borin*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Garganey	*Anas querquedula*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Goldcrest	*Regulus regulus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Golden Eagle	*Aquila chrysaetos*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.

Golden Plover	*Pluvialis apricaria*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Grasshopper Warbler	*Locustella naevia*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Great Black-backed Gull	*Larus marinus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Great Cormorant	*Phalacrocorax carbo*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Great Crested Grebe	*Podiceps cristatus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Great Skua	*Catharacta skua*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Great Spotted Woodpeck	*Dendrocopos major*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Great Tit	*Parus major*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Green Woodpecker	*Picus viridis*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
Green-winged Teal	*Anas crecca*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Grey Heron	*Ardea cinerea*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Grey Wagtail	*Motacilla cinerea*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Hawfinch	*Coccothraustes coccothra*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Hen Harrier	*Circus cyaneus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Herring Gull	*Larus argentatus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Honey-buzzard	*Pernis apivorus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Hooded Crow	*Corvus cornix*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Horned Grebe	*Podiceps auritus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
House Martin	*Delichon urbicum*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
House Sparrow	*Passer domesticus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Jackdaw	*Corvus monedula*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.

Leach's Petrel	*Oceanodroma leucorhoa*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Lesser Black-backed Gul	*Larus fuscus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Lesser Spotted Woodpec	*Dendrocopos minor*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
Lesser Whitethroat	*Sylvia curruca*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Linnet	*Carduelis cannabina*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Little Grebe	*Tachybaptus ruficollis*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Little Ringed Plover	*Charadrius dubius*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Little Tern	*Sterna albifrons*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Long-eared Owl	*Asio otus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Long-tailed Tit	*Aegithalos caudatus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Magpie	*Pica pica*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Manx Shearwater	*Puffinus puffinus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Marsh Harrier	*Circus aeruginosus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Marsh Tit	*Parus palustris*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
Marsh Warbler	*Acrocephalus palustris*	Extirpated	Extirpated	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
Meadow Pipit	*Anthus pratensis*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Merlin	*Falco columbarius*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Mew Gull	*Larus canus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Mistle Thrush	*Turdus viscivorus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Montagu's Harrier	*Circus pygargus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Nightjar	*Caprimulgus europaeus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.

Northern Fulmar	*Fulmarus glacialis*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Northern Gannet	*Morus bassanus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Northern Lapwing	*Vanellus vanellus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Northern Pintail	*Anas acuta*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Northern Shoveler	*Anas clypeata*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Northern Wheatear	*Oenanthe oenanthe*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Nuthatch	*Sitta europaea*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
Parasitic Jaeger	*Stercorarius parasiticus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Parrot Crossbill	*Loxia pytyopsittacus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
Peregrine Falcon	*Falco peregrinus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Pied Avocet	*Recurvirostra avosetta*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Raven	*Corvus corax*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Razorbill	*Alca torda*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Red Crossbill	*Loxia curvirostra*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Red-billed Chough	*Pyrrhocorax pyrrhocorax*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Red-breasted Merganser	*Mergus serrator*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Red-necked Phalarope	*Phalaropus lobatus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Red-throated Loon	*Gavia stellata*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Redwing	*Turdus iliacus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Reed Bunting	*Emberiza schoeniclus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Reed Warbler	*Acrocephalus scirpaceus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.

Ring Ouzel	*Turdus torquatus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Rock Pipit	*Anthus petrosus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Rock Ptarmigan	*Lagopus muta*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
Rook	*Corvus frugilegus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Roseate Tern	*Sterna dougallii*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Ruff	*Philomachus pugnax*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Sand Martin	*Riparia riparia*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Sandwich Tern	*Sterna sandvicensis*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Scottish Crossbill	*Loxia scotica*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
Sedge Warbler	*Acrocephalus schoenobae*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Short-eared Owl	*Asio flammeus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Snow Bunting	*Plectrophenax nivalis*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Song Thrush	*Turdus philomelos*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Spotted Crake	*Porzana porzana*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Spotted Flycatcher	*Muscicapa striata*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Stock Dove	*Columba oenas*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Stonechat	*Saxicola torquatus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Stone-curlew	*Burhinus oedicnemus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Storm Petrel	*Hydrobates pelagicus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Tawny Owl	*Strix aluco*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Tree Pipit	*Anthus trivialis*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.

Tufted Duck	*Aythya fuligula*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Turtle Dove	*Streptopelia turtur*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Twite	*Carduelis flavirostris*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Water Rail	*Rallus aquaticus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Whimbrel	*Numenius phaeopus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Whinchat	*Saxicola rubetra*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
White Wagtail	*Motacilla alba*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
White-throated Dipper	*Cinclus cinclus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Whooper Swan	*Cygnus cygnus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Willow Ptarmigan	*Lagopus lagopus*	Naturalised	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Willow Tit	*Parus montanus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
Willow Warbler	*Phylloscopus trochilus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Wood Sandpiper	*Tringa glareola*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Wood Warbler	*Phylloscopus sibilatrix*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Woodlark	*Lullula arborea*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.
Woodpigeon	*Columba palumbus*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Wren	*Troglodytes troglodytes*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Yellow Wagtail	*Motacilla flava*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Yellowhammer	*Emberiza citrinella*	Native	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Gadwall	*Anas strepera*	Naturalised	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.
Greylag Goose	*Anser anser*	Naturalised	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, nibirds.blogspot.com 160: 190-240.

Mallard	*Anas platyrhynchos*	Naturalised	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com	
Rock Dove	*Columba livia*	Naturalised	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com	
Barnacle Goose	*Branta leucopsis*	Naturalised	Naturalised	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com	
Canada Goose	*Branta canadensis*	Naturalised	Naturalised	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com	
Common Pheasant	*Phasianus colchicus*	Naturalised	Naturalised	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com	
Egyptian Goose	*Alopochen aegyptiaca*	Naturalised	Naturalised	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.	
Golden Pheasant	*Chrysolophus pictus*	Naturalised	Naturalised	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.	
Little Owl	*Athene noctua*	Naturalised	Naturalised	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com	
Mandarin Duck	*Aix galericulata*	Naturalised	Naturalised	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com	
Mute Swan	*Cygnus olor*	Naturalised	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com	Birkhead and Perrins, 1986. The Mute Swan: London, U. K., Croom Helm Ltd
Red-crested Pochard	*Netta rufina*	Naturalised	Naturalised	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com	
Red-legged Partridge	*Alectoris rufa*	Naturalised	Naturalised	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com	
Rose-ringed Parakeet	*Psittacula krameri*	Naturalised	Naturalised	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.	
Ruddy Duck	*Oxyura jamaicensis*	Naturalised	Naturalised	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com	
Snow Goose	*Chen caerulescens*	Naturalised	Naturalised	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com	
Black-winged Stilt	*Himantopus himantopus*	Recent (re)colonist	Recent (re)colonist	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com	rbbp.org.uk
Cattle Egret	*Bubulcus ibis*	Recent (re)colonist	Recent (re)colonist	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com	rbbp.org.uk
Cetti's Warbler	*Cettia cetti*	Recent (re)colonist	Recent (re)colonist	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.	rbbp.org.uk
Collared Dove	*Streptopelia decaocto*	Recent (re)colonist	Recent (re)colonist	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com	rbbp.org.uk
Eurasian Spoonbill	*Platalea leucorodia*	Recent (re)colonist	Recent (re)colonist	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240. nibirds.blogspot.com	rbbp.org.uk
European Serin	*Serinus serinus*	Recent (re)colonist	Recent (re)colonist	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.	rbbp.org.uk

Firecrest	*Regulus ignicapilla*	Recent (re)colonist	Recent (re)colonist	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.	nibirds.blogspot.com	rbbp.org.uk	
Great Egret	*Casmerodius albus*	Recent (re)colonist	Recent (re)colonist	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.	nibirds.blogspot.com	rbbp.org.uk	
Little Bittern	*Ixobrychus minutus*	Recent (re)colonist	Recent (re)colonist	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.	nibirds.blogspot.com	rbbp.org.uk	
Little Egret	*Egretta garzetta*	Recent (re)colonist	Recent (re)colonist	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.	nibirds.blogspot.com	rbbp.org.uk	
Mediterranean Gull	*Larus melanocephalus*	Recent (re)colonist	Recent (re)colonist	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.	nibirds.blogspot.com	rbbp.org.uk	
Bam Owl	*Tyto alba*	Rewilding	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.	nibirds.blogspot.com	barnowltrust.org.uk	
Black-tailed Godwit	*Limosa limosa*	Rewilding	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.	nibirds.blogspot.com	projectgodwit.org.uk	
Cirl Bunting	*Emberiza cirlus*	Rewilding	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.		Jeffs, Cath, et al. "Reintroducing the cirl bunting to Cornwall." British Birds (2016).	
Corncrake	*Crex crex*	Rewilding	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.	nibirds.blogspot.com	rspb.org.uk/birds-and-wildlife/wildlife-guides/bird-a-z/corncrake/conservation/	
Grey Partridge	*Perdix perdix*	Rewilding	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.	nibirds.blogspot.com	gwct.org.uk/advisory/guides/re-establishing-grey-partridges-through-releasing	
Osprey	*Pandion haliaetus*	Rewilding	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.	nibirds.blogspot.com	wildlifetrusts.org	
Red Kite	*Milvus milvus*	Rewilding	Native	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.	nibirds.blogspot.com	rspb.org.uk/birds-and-wildlife/wildlife-guides/bird-a-z/red-kite/conservation/	
Common Crane	*Grus grus*	Rewilding	Recent (re)colonist	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.	nibirds.blogspot.com	thegreatcraneproject.org.uk	wwt.org.uk/our-work/projects/reintroducing-common-cranes rbbp.org.uk
Northern Goshawk	*Accipiter gentilis*	Rewilding	Recent (re)colonist	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.	nibirds.blogspot.com	scottishraptorstudygroup.org/raptors/goshawk	rbbp.org.uk
Dalmatian Pelican	*Pelecanus crispus*	Rewilding	Rewilding	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.	nibirds.blogspot.com	rewildingbritain.org.uk	
Great Bustard	*Otis tarda*	Rewilding	Rewilding	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.		greatbustard.org/the-project/	rspb.org.uk/our-work/conservation/projects/reintroducing-the-great-bustard-to-southern-england
Western Capercaillie	*Tetrao urogallus*	Rewilding	Rewilding	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.	nibirds.blogspot.com	Steven R. Ewing et al. (2012) The size of the Scottish population of Capercaillie Tetrao urogallus: results of the fourth national survey, Bird Study, 59:2, 126-138, DOI: 10.1080/00063657.2011.652937	
White Stork	*Ciconia ciconia*	Rewilding	Rewilding	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.	nibirds.blogspot.com	whitestorkproject.org	
White-tailed Eagle	*Haliaeetus albicilla*	Rewilding	Rewilding	McInemy, C.J. et al (2018), The British List: A Checklist of Birds of Britain (9th edition). Ibis, 160: 190-240.	nibirds.blogspot.com	rspb.org.uk/our-work/conservation/projects/east-scotland-sea-eagles/	

Table S2 Category of mammals in the UK.

English	Scientific	Category	Reference 1	Reference 2
Alcathoe bat	*Myotis alcathoe*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
American mink	*Neovison vison*	Naturalised	mammal.org.uk/species-hub/uk-mammal-list/	
Arctic fox	*Vulpes lagopus*	Extirpated	Yalden, Derek. The history of British mammals. A&C Black, 2010.	
Arctic lemming	*Dicrostonyx torquatus*	Extirpated	Yalden, Derek. The history of British mammals. A&C Black, 2010.	
Badger	*Meles meles*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Bank vole	*Myodes glareolus*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Barbastelle bat	*Barbastella barbastellus*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Bechsteins bat	*Myotis bechsteinii*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Black rat	*Rattus rattus*	Introduced	mammal.org.uk/species-hub/uk-mammal-list/	
Brandts bat	*Myotis brandtii*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Brown hare	*Lepus europaeus*	Naturalised	mammal.org.uk/species-hub/uk-mammal-list/	
Brown long-eared bat	*Plecotus auritus*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Brown rat	*Rattus norvegicus*	Naturalised	mammal.org.uk/species-hub/uk-mammal-list/	
Chinese water deer	*Hydropotes inermis*	Naturalised	mammal.org.uk/species-hub/uk-mammal-list/	
Common pipstrelle bat	*Pipistrellus pipistrellus*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Common shrew	*Sorex araneus*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Common vole	*Microtus arvalis*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Daubentons bat	*Myotis daubentonii*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Edible dormouse	*Glis glis*	Naturalised	mammal.org.uk/species-hub/uk-mammal-list/	
Eurasian beaver	*Castor fiber*	Rewilding	mammal.org.uk/species-hub/uk-mammal-list/	wildlifetrusts.org/saving-species/beavers
Eurasian brown bear	*Ursus arctos*	Extirpated	Yalden, Derek. The history of British mammals. A&C Black, 2010.	
Eurasian elk	*Alces alces*	Rewilding	rewildingbritain.org.uk	
Eurasian lynx	*Lynx lynx*	Rewilding	https://lynxuk.org/	
Eurasian wolf	*Canis lupus*	Extirpated	Yalden, Derek. The history of British mammals. A&C Black, 2010.	
European bison	*Bison bonasus*	Rewilding	kentwildlifetrust.org.uk/wilderblean	
European mole	*Talpa europaea*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
European rabbit	*Oryctolagus cuniculus*	Naturalised	mammal.org.uk/species-hub/uk-mammal-list/	
Fallow deer	*Dama dama*	Naturalised	mammal.org.uk/species-hub/uk-mammal-list/	
Feral horse	*Equus ferus*	Rewilding	mammal.org.uk/species-hub/uk-mammal-list/	kentwildlifetrust.org.uk/
Field vole	*Microtus agrestis*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Greater horseshoe bat	*Rhinolophus ferrumequinum*	Native	mammal.org.uk/species-hub/uk-mammal-list/	

Greater mouse-eared bat	*Myotis myotis*	Extirpated	Yalden, Derek. The history of British mammals. A&C Black, 2010.	
Greater white-toothed shrew	*Crocidura russula*	Naturalised	mammal.org.uk/species-hub/uk-mammal-list/	
Grey long-eared bat	*Plecotus austriacus*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Grey squirrel	*Sciurus carolinensis*	Naturalised	mammal.org.uk/species-hub/uk-mammal-list/	
Harvest mouse	*Micromys minutus*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Hazel dormouse	*Muscardinus avellanarius*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Hedgehog	*Erinaceus europaeus*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
House mouse	*Mus musculus*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Leislers bat	*Nyctalus leisleri*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Lesser horseshoe bat	*Rhinolophus hipposideros*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Lesser white-toothed shrew	*Crocidura suaveolens*	Naturalised	mammal.org.uk/species-hub/uk-mammal-list/	
Mountain hare	*Lepus timidus*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Muskox	*Ovibos moschatus*	Extirpated	Yalden, Derek. The history of British mammals. A&C Black, 2010.	
Narrow-headed vole	*Microtus gregalis*	Extirpated	Yalden, Derek. The history of British mammals. A&C Black, 2010.	
Nathusius pipistrelle bat	*Pipistrellus nathusii*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Natterers bat	*Myotis nattereri*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Noctule bat	*Nyctalus noctula*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Norway lemming	*Lemmus lemmus*	Extirpated	Yalden, Derek. The history of British mammals. A&C Black, 2010.	
Otter	*Lutra lutra*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Pine marten	*Martes martes*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Polecat	*Mustela putorius*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Pygmy shrew	*Sorex minutus*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Red deer	*Cervus elaphus*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Red fox	*Vulpes vulpes*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Red squirrel	*Sciurus vulgaris*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Red-necked wallaby	*Macropus rufogriseus*	Introduced	mammal.org.uk/species-hub/uk-mammal-list/	
Reeves muntjac deer	*Muntiacus reevesi*	Naturalised	mammal.org.uk/species-hub/uk-mammal-list/	
Reindeer	*Rangifer tarandus*	Rewilding	mammal.org.uk/species-hub/uk-mammal-list/	https://www.cairngormreindeer.co.uk/
Roe deer	*Capreolus capreolus*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Root vole	*Microtus oeconomus*	Extirpated	Yalden, Derek. The history of British mammals. A&C Black, 2010.	
Saiga antelope	*Saiga tatarica*	Extirpated	Yalden, Derek. The history of British mammals. A&C Black, 2010.	
Serotine bat	*Eptesicus serotinus*	Native	mammal.org.uk/species-hub/uk-mammal-list/	

Sika deer	*Cervus nippon*	Naturalised	mammal.org.uk/species-hub/uk-mammal-list/	
Soprano pipistrelle bat	*Pipistrellus pygmaeus*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Steppe pika	*Ochotona pusilla*	Extirpated	Yalden, Derek. The history of British mammals. A&C Black, 2010.	
Stoat	*Mustela erminea*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Water shrew	*Neomys fodiens*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Water vole	*Arvicola amphibius*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Weasel	*Mustela nivalis*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Whiskered bat	*Myotis mystacinus*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Wild boar	*Sus scrofa*	Rewilding	mammal.org.uk/species-hub/uk-mammal-list/	mammal.org.uk/2015/03/re-establishment-of-wild-boar-in-britain
Wildcat	*Felis silvestris*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Wolverine	*Gulo gulo*	Extirpated	Yalden, Derek. The history of British mammals. A&C Black, 2010.	
Wood mouse	*Apodemus sylvaticus*	Native	mammal.org.uk/species-hub/uk-mammal-list/	
Yellow-necked mouse	*Apodemus flavicollis*	Native	mammal.org.uk/species-hub/uk-mammal-list/	

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Appendix D

Migratory waterfowl's responses to habitat degradation

Species-dependent effects of habitat degradation in relation to seasonal distribution of migratory waterfowl in the East Asian–Australasian Flyway

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Abstract

Context Migratory species' resilience to landscape changes depends on spatial patterns of habitat degradation in relation to their migratory movements, such as the distance between breeding and non-breeding areas, and the location and width of migration corridors.

Objectives We investigated to what extent the impact of habitat degradation depended on the seasonal distributions of migratory waterfowl.

Methods Using logistic regression, we selected wetland sites for eight waterfowl species in the East Asian–Australasian Flyway (EAAF) by calculating the probabilities of species occurrence per wetland site in relation to environmental factors. We quantified landscape metrics related to habitat degradation within these wetland sites. We used general linear models to test for differences in the effects of habitat degradation on waterfowl species with different migration extents and at different latitudes.

Results The patterns of habitat degradation differed spatially across the EAAF and affected species to a different degree. Species with shorter and broader migration corridors (*Anser cygnoid* and *A. anser*) could benefit from improved habitat conditions in the west of the EAAF. Species with longer and narrower migration corridors (*Cygnus columbianus*, *A. fabalis*, *A. albifrons*, *A. erythropus*, *Anas crecca*, and *Anas acuta*) were under higher risk of habitat degradation in the coastal regions of China and Japan.

Conclusions Migratory species with longer and narrower migration corridors are more affected by habitat degradation, because they might have fewer

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alternative stopover sites at similar latitude. Our findings improve the understanding of species-specific effects of environmental changes on migratory species, and defines critical and endangered wetland sites, and vulnerable species.

Keywords Seasonal distribution · Species trait · Migratory waterfowl · Habitat loss · Fragmentation · Isolation · East Asian–Australasian Flyway · Migratory connectivity · Wetland

Introduction

Habitat loss is one of the most important factors causing population declines in migratory birds (Sanderson et al. 2006). Habitat degradation along migration routes has been linked to decreases in populations of a number of migratory bird populations (Iwamura et al. 2013; Studds et al. 2017). Wetlands, the main habitat for migratory waterfowl species, are among the most threatened habitats worldwide, and nearly half of the world's wetlands have disappeared as a result of the expansion of human activities (Millennium Ecosystem Assessment 2005; Silva et al. 2007). China has lost 33% of its wetland area from 1978 to 2008, although the trend of wetland loss is slowing down lately (Niu et al. 2012). Hence, in the last decades, ecosystem service values of natural areas have declined substantially as a consequence of wetland loss and degradation (Wang et al. 2006).

Landscape composition and configuration of suitable habitats affect species occurrence and richness (Guadagnin and Maltchik 2007; Mora et al. 2011; Xu et al. 2014; Zhang et al. 2018). Availability of wetlands and waterbodies, wetland size, and wetland connectivity positively influence waterfowl species occurrence and species richness, while wetlands in proximity to rice fields, total rice field area, and wetland isolation have negative effects (Guadagnin and Maltchik 2007; Zhang et al. 2018). Therefore, waterfowl habitat degradation can be quantified by land cover changes and dynamics in landscape variables of wetland sites along migration corridors (Van Eerden et al. 2005; Tian et al. 2008). However, because of limited attention to the spatio-temporal dynamics of wetland sites along migration routes (Dong et al. 2015), it is currently unknown how current trends of habitat degradation influence migratory waterfowl species.

The East Asian–Australasian Flyway is one of the nine major waterbird flyways globally. The flyway holds over 50 million migratory waterbirds, including 51 threatened or near-threatened species (EAAFP 2017). Because of the loss and degradation of suitable habitats, resulting from rapid economic development and human disturbance, population sizes for many waterfowl species in the northern part of the flyway have declined rapidly (Syroechkovskiy 2006; Cao et al. 2008, 2010; de Boer et al. 2011; Si et al. 2018).

The delineated range of the East Asian–Australasian Flyway is rather broad, so the species that use it display considerable variability in the spatial patterns of their breeding, non-breeding, and stopover sites. For instance, the swan goose (*Anser cygnoid*) breeds in both eastern and western Mongolia (Batbayar et al. 2013), while the greater white-fronted goose (*Anser albifrons*) is an Arctic-breeding migrant with a distribution extending to the Lena Delta, Siberia. However, the non-breeding grounds of the greater white-fronted goose in the Yangtze River Basin overlap with those of swan goose (Si et al. 2018). The falcated duck (*Mareca falcata*) uses both the eastern and central parts of the East Asian–Australasian Flyway, while the common teal (*Anas crecca*) is restricted to the eastern part of the flyway (Takekawa et al. 2010).

The spatial extent of these waterfowl species' seasonal distributions probably influences the degree to which they are affected by habitat degradation. For instance, population sizes of long-distance migratory species decline more rapidly than those of short-distance migratory species (Morrison et al. 2013). Independently of the distance of migration, species with broader dispersal ranges are less prone to population declines compared to those whose ranges are restricted, because of spatial variation in habitat degradation (Gilroy et al. 2016). In addition, the underlying patterns of habitat loss also make a difference in species-specific consequences of habitat degradations, e.g., a small amount of habitat loss in certain crucial stopover sites can trigger severe impacts (Weber et al. 1999; Runge et al. 2014). The resilience of waterfowl species to environmental changes varies because of spatial patterns in habitat degradation and differences in the species' seasonal

distributions. However, habitat degradation has not been analysed for its species-specific effects as a consequence of the spatial variation in migration patterns.

In this study, we quantified the spatial patterns of habitat degradation in wetland sites, in relation to the seasonal distributions of eight waterfowl species. Wetland sites can be located in breeding grounds, non-breeding grounds, or stopover sites in a species' migration route. First, we selected all wetland sites where each species was likely to occur in the distribution ranges of each waterfowl species based on the modelled relationships between species occurrence and environmental factors (hereafter suitable wetland sites). Second, within the ranges of suitable wetland sites, as metrics of habitat degradation, we quantified the availability of water area, grassland, and wetland, and quantified wetland fragmentation and isolation, and changes in agricultural resources. Finally, we explored the species-specific effects of habitat degradation in relation to the species' migratory extents. The risk from habitat degradation is determined by how the species' distribution overlaps with the spatial distribution of habitat changes. We expect that migratory species with a longer and narrower migration corridors are more likely to be affected by habitat degradation. The results can provide a better understanding of the underlying mechanisms of how environmental changes affect different migratory species, so that targeted conservation plans can be developed for critical and endangered wetland sites and vulnerable species.

Methods

Study area

The East Asian–Australasian Flyway identified by the global monitoring program of Wetland International stretches across 22 countries, covering East Asia, Southeast Asia, Australia, and New Zealand, and northern areas from the Taimyr Peninsula in Russia to Alaska (EAAFP 2017). Unlike Artic-breeding shorebirds that spend the non-breeding season in Australia and New Zealand, most of the Arctic-breeding waterfowl in the East Asian–Australasian Flyway migrate only as far south as China (Birdlife International and NatureServe 2015). We focused on the waterfowl populations overwintering in the Yangtze River Basin, one of the most important non-breeding grounds in the flyway. Therefore, the study area extended from the Yangtze River Basin to the northern part of the East Asian–Australasian Flyway (Appendix S1). Overall, the study area overlaps with six countries: China, Mongolia, North Korea, South Korea, Japan, and Russia.

Study species

The wetlands in the Yangtze River Basin are key non-breeding sites of eleven goose, swan, and dabbling duck species (Cao et al. 2010), including tundra swan (*Cygnus columbianus*), swan goose, bean goose (*Anser fabalis*), greater white-fronted goose, lesser white-fronted goose (*Anser erythropus*), greylag goose (*Anser anser*), falcated duck, Baikal teal (*Sibirionetta formosa*), common teal, spot-billed duck (*Anas poecilorhyncha*), and northern pintail (*Anas acuta*). Eight of the eleven species were included in our analysis. Falcated duck, Baikal teal, and spot-billed duck were excluded because of a lack of detailed information about their breeding distribution (Birdlife International and NatureServe 2015).

Data

Bird data

Breeding and non-breeding ranges of the eight waterfowl species were obtained from bird species distribution maps of the world (v5.0), produced by Birdlife International (Birdlife International and NatureServe 2015). Information on the occurrence of the eight Anatidae species within the study area was obtained from the eBird citizen-science database: eBird Basic Dataset (v1.5), which provides species scientific name, population count, latitude, longitude, and date and time of bird observations (Sullivan et al. 2014; Cornell Lab of Ornithology 2016). All records from 1992 to 2016 were included in the analysis, except for data that were not verified by eBird editors. Duplicate records of the same species, location, date, and time of observations were excluded. The records of the eight study species with in the study area were included in the analysis. In total, there were 89 locations with observations of greylag goose, 197 for swan goose, 173 for bean goose, 357 for greater white-fronted

goose, 57 for lesser white-fronted goose, 223 for tundra swan, 408 for common teal, and 1110 for northern pintail within the study area.

Data for environmental factors

The polygons of lakes, reservoirs, and smaller water bodies (called 'wetland sites' here) with a surface area $\geq$ 0.1 km^2 were obtained from the Global Lakes and Wetlands Database (GLWD-1 and GLWD-2; accessed on 22-02-2017; (Lehner and Döll 2004). The 500-m-resolution elevation data was obtained from Jonathan de Ferranti's Digital Elevation Data site (accessed on 07-03-2017), which combines data from multiple sources, including ASTER Global Digital Elevation Map (ASTER GDEM), gap-filling Shuttle Radar Topography Mission (known as SRTM), and contour maps (de Ferranti 2014). The area of food resources (grassland and cropland) around each lake was derived from the ESA CCI 300-m global land cover products (v2.0.7) of the year 1992 (European Space Agency 2017).

Land cover data for landscape metrics

We used land cover maps for 1992 and 2012 from the European Space Agency (ESA) CCI 300-m annual global land cover products (European Space Agency 2017) to quantify the spatial patterns of habitat degradation. The land cover was reclassified into six types: water (water bodies), woodland (tree cover and shrubland), grassland (herbaceous cover, grasslands, and lichens and mosses), cropland (agricultural crops), bareland (bare areas, sparse herbaceous cover, unconsolidated bare areas, and permanent snow and ice), and urban and built-up areas (urban areas and consolidated bare areas). The croplands north of the Amur were not included in the analysis for two reasons. First, there are few croplands in those regions because of an unsuitable climate and low human density. Second, small patches of croplands could scarcely be detected by the 300-m-resolution remote sensing devices, and the clear-cuts created by logging activities and forest fires, a widespread event in Siberian forests, can be misclassified as cropland.

Identification of suitable wetland sites

The selection of suitable wetland sites in the distribution ranges of each study species was achieved by calculating the probabilities of species occurrence in relation to environmental factors. We assumed that the migratory birds do not travel further north than their breeding ranges or further south than their non-breeding ranges. Therefore, for each species, we first selected all wetlands that fell within the study area (Appendix S1) as well as between their northernmost extent of the breeding range and southernmost extent of their non-breeding range (Birdlife International and NatureServe 2015). Habitat selection by migratory waterfowl is mainly based on availability and suitability of wetlands and influenced by the type and extent of surrounding land-use types (Davis et al. 2014). Therefore, we built a logistic regression model using the presence/absence of a study species in each wetland, in relation to lake area (km^2), elevation (m), x coordinates (m; to represent the East–West gradient under the azimuthal equidistant projection) of lakes, and surrounding extent of suitable foraging areas, to predict the suitable wetland sites for each study species. Lakes with one or more observations of a study species were defined as presence records. We then randomly generated an equal number of absence records in the lakes where ebirder visited but without observations of the specific study species. Distances between roosting and foraging sites of waterfowl species in general do not exceed their maximum foraging flight distance (Beatty et al. 2014), so the surrounding extent of foraging areas was measured by the area (km^2) of grassland and cropland within a 32.5-km radius buffer around each lake, which is the maximum mean foraging flight distances of ducks and geese (Johnson et al. 2014). Both x coordinates, as measured by the center x coordinate of each lake, and the squared x coordinate, were added to the model because we assumed a dome-shaped relationship between the chance of a wetland being used by a specific species and the x-coordinate, for example, higher near the coast or higher in the center of their migration extent than at the edge.

For each species, the best model with the smallest bias-adjusted Akaike's information criterion was selected (Burnham and Anderson 2003). By classifying the predicted probability of occurrence as presence or absence with a cutoff value of 50%, the accuracy of

the models was calculated by summing the number of true positive cases (classified by the model as presence and the species is present in reality) and true negatives (classified by the model as absence and the species is absent in reality) divided by total number of cases (Olson and Delen 2008). A wetland site was defined as suitable when the predicted probability of presence of the specific species exceeded 50% (Appendix S3). The wetland area in subsequent analyses included these suitable lakes and a 32.5-km buffer around each of these suitable lakes (Olson and Delen 2008).

All distances and coordinates were calculated under the azimuthal equidistant projection, and all areas were calculated under the cylindrical equal area. Calculations of the environmental factors were performed in ArcMap 10.2.1 (ESRI, San Diego, CA, USA). Logistic regressions were performed with package 'lme4' (Bates et al. 2014), and model selections were performed with package 'MuMIn'(Burnham and Anderson 2003) in R 3.3.3.

Quantification of habitat degradation

To quantify how habitats in these suitable wetland sites changed from 1992 to 2012, we calculated six landscape metrics including availability of water area, grassland, and wetland, and quantified wetland fragmentation and isolation, and changes in agriculture resources in 1992 and 2012, respectively (Table 1). Water and surrounding grasslands were aggregated into wetland properties, as both the area of open water and surrounding grasslands affect the suitability of a wetland for waterfowl (Horn et al. 2005; Beatty et al. 2014). The size of a wetland is a key predictor for waterfowl species richness, and wetland connectivity and isolation are additional landscape metrics affecting waterfowl habitat quality (Guadagnin and Maltchik 2007; Zhang et al. 2015).

All landscape metrics were measured per suitable wetland site in each 100 × 100 km grid cell, as the upper quartile of scales at which habitat configuration affects the distribution of species is approximately 100 km, partly because the maximum radius of a species' foraging flight is generally smaller than 50 km (Ackerman et al. 2006; McGill 2010; Si et al. 2011; Johnson et al. 2014). Water, grassland, and wetland availability were measured by the total area of water bodies, grassland, and wetlands, respectively. Wetland fragmentation was measured by the change in mean patch area of wetlands. Wetland isolation was quantified by the change in the Proximity Index, which equals the sum of the wetland patch area divided by the squared edge-to-edge distance between a wetland patch and the wetland patches whose edges are within 32.5 km around the specific patch (Gustafson and Parker 1992), as:

$$Proximity\ index = \sum_{s=1}^{n} \frac{a_{ijs}}{d_{ijs}^2}$$

where n equals number of wetland patches within the suitable wetland sites in each 200 × 200 km grid cell; a_{ijs} is the area of wetland patch ij, which is within in a distance of 32.5 km around focal wetland patch s; d_{ijs} is the edge-to-edge distance between wetland patch ij and focal wetland patch s. The availability of agricultural resources was quantified by the total area of cropland.

All calculations were conducted under the azimuthal equidistant projection. Geographic data for calculating landscape metrics were prepared with ArcMap 10.2.1 (ESRI, San Diego, CA, USA). Fragstats 4.2 (McGarigal and Marks 1995) was used to calculate landscape metrics.

Exploration of species variation affected by habitat degradation

Habitat degradation was quantified by the change ratios of the six landscape metrics from 1992 to 2012 in each 100 × 100 km grid cell, as:

$$Change\ ratio = \ln\left(\frac{V_{2012}}{V_{1992}}\right)$$

where V_{1992} and V_{2012} is the value of each landscape metric in 1992 and 2012, respectively. To better understand the latitudinal, national, and species-specific patterns of habitat degradation, the mean change ratio of each landscape metric in each 5-degree latitudinal zone (each zone is 5-degree wide), each country, and in each breeding, non-breeding, and stopover area (the suitable wetland sites in between their breeding and non-breeding ranges) of each study species was calculated by overlapping the species' ranges with the calculated six landscape metrics maps (grid cell: 100 × 100 km).

Three general linear models (GLMs) were applied to test (1) whether patterns of wetland degradation

Table 1 Landscape variables associated with waterfowl habitat degradation

Variable	Index for	Description
Total area (ha)	Wetland availability	Wetland size
Mean area (ha)	Wetland Fragmentation	The average wetland patch area
Proximity Index	Wetland Isolation	A measurement of relative isolation of the wetland patches. High value indicates habitat patches are connected to each other within a buffer distance, while low Proximity Index value indicates they are isolated from each other (Gustafson and Parker 1992)
Total water area (ha)	Water area availability	A measurement of availability of water surface as roosting habitats
Total grassland area (ha)	Grassland availability	A measurement of availability of grasslands as primary food resources
Total crop area (ha)	Agriculture Resources	A measurement of availability of croplands as additional food resources

All landscape metrics were measured in the suitable wetland sites in each 100 × 100 km grid cell. Wetland properties include water and surrounding grassland. The changes were quantified by change ratios from 1992 to 2012

change over latitude and (2) whether the patterns differs among species with different migration extent (i.e., species with shorter and broader migration corridors versus those with longer and narrower migration corridors). The three dependent variables were the mean of absolute changes in the change ratios of wetland availability, fragmentation, and isolation, respectively. Independent variables of each model included one continuous variable (latitude) and one categorical variable (the species catalogue with two classes; i.e., '1' is species with longer and narrower migration corridors; '2' is species with shorter and broader migration corridors). We defined six out of the eight study species (tundra swan, bean goose, greater white-fronted goose, lesser white-fronted goose, common teal, and northern pintail) as species with longer and narrower migration corridors, with their seasonal distribution extending from the Lower Yangtze to Siberia. The swan goose and greylag goose were classified as species with shorter and broader migration corridors that breed in Mongolian regions and occupy more western parts of the flyway compared to the first group of species (Fig. 1). This classification is in agreement with previous findings (Morrison et al. 2013; Gilroy et al. 2016).

The changes in landscape variables in different regions was calculated with ArcMap 10.2.1. The basic statistics were calculated in R 3.3.3, and the GLMs were carried out with package 'lme4' (Bates et al. 2014) in R 3.3.3.

Results

Environmental factors and the presence of waterfowl in wetland sites

According to the best models, the presence of all goose and duck species was positively related to area of lakes, and the presence of all species (except lesser white-fronted goose) was positively related to surrounding food resources (i.e., grass and crop resources; Table 2). The probability of presence for greater white-fronted goose, lesser white-fronted goose, tundra swan, and northern pintail increased with decreasing elevation (Table 2).

Habitat degradation in the flyway

In the predicted suitable wetland sites (Fig. 1), for all eight species, 4% of the landscape was covered by water, and 26% and 21% of the landscape by grassland and cropland, respectively. The water area in suitable wetland sites in both non-breeding and breeding ranges of all eight species decreased during the 1992–2012 period, mainly in Southeast China, South Korea, Japan, Mongolia, and Northeast Russia (Fig. 2a).

As illustrated by the negative change in corresponding landscape variables in each grid, 43, 51, and 45% of the landscape experienced wetland loss, fragmentation, and isolation, respectively (Fig. 2).

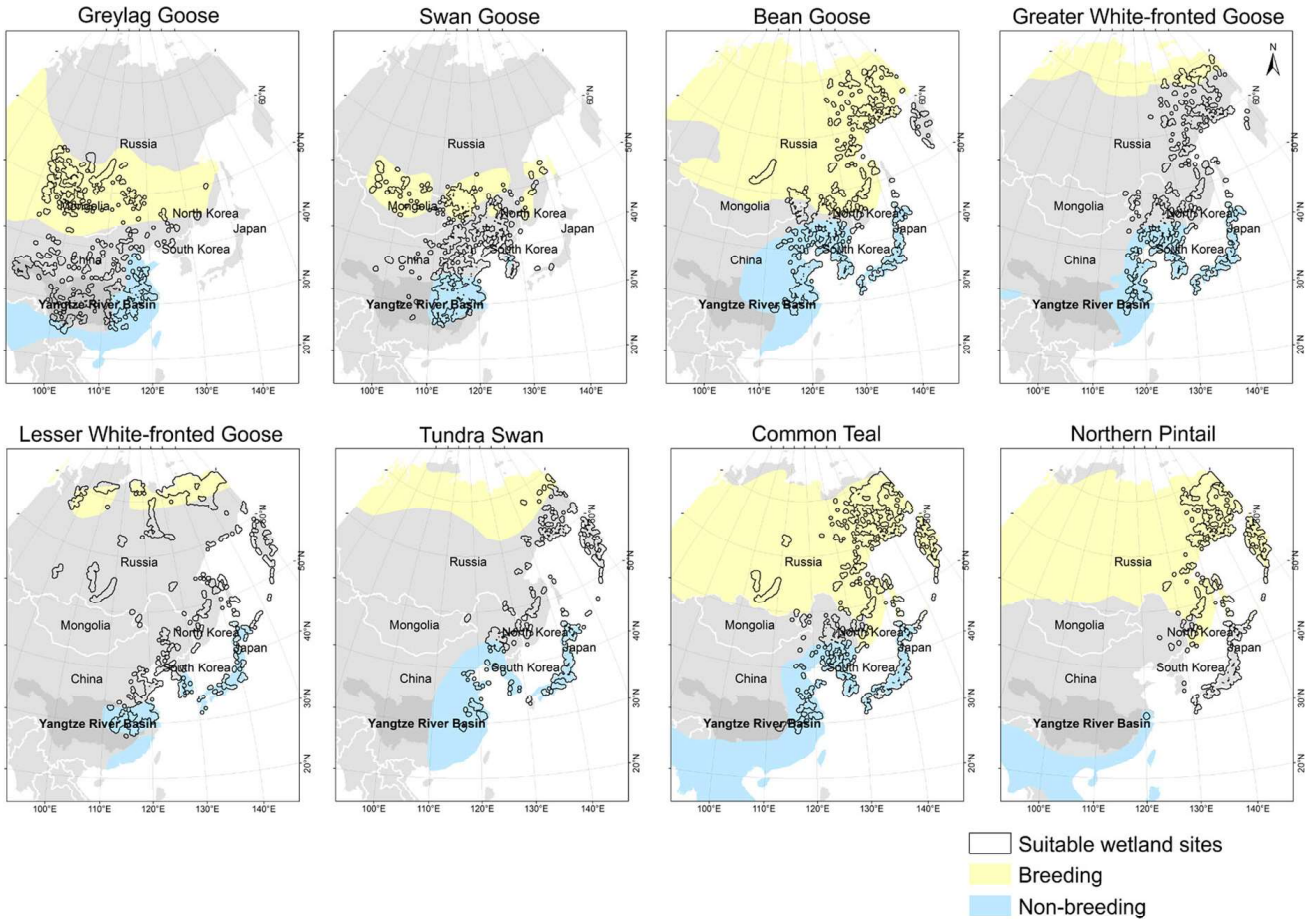

Fig. 1 Suitable wetland sites (hollow polygon with black border) for eight waterfowl species in the East Asian-Australasian Flyway. The ranges of suitable wetland sites were used for subsequent analysis, and included suitable lakes and a 32.5-km buffer around each of the suitable lakes

The three processes of wetland degradation happened simultaneously in 27% of the landscape, specifically in their non-breeding grounds in the Middle and Lower Yangtze River, Lower Yellow River, and Japan (Fig. 2). Habitat availability improved in inland regions, including the Upper Yellow River, Korea, Mongolia, and Russia, which are important breeding grounds for the study species, as indicated by an increase in wetland area and a decrease in the level of wetland isolation (Appendix S7).

Species-dependent effect of habitat degradation

The eight species were all exposed to wetland loss, fragmentation, and isolation in their non-breeding grounds in China and Japan, but their breeding grounds improved in both Mongolia and Russia. Although the configuration of wetlands improved in the stopover areas of the bean goose, greater white-fronted goose, and tundra swan, who pass both China and Russia during migration, the other species were affected by wetland loss, fragmentation, and isolation in their stopover areas, especially for those species with stopover areas in China and Japan (Appendices S3 and S4). Generally, the migratory species were affected by habitat degradation in the southern part of their seasonal distributions, and their habitat availability improved in the northern part (Fig. 3).

During 1992–2012, the wetland availability increased (or decreased less rapidly) with increasing latitude (GLM, $\beta = 0.004$, $t = 17.66$, $DF = 4619$, $P < 0.01$), and species with shorter and broader migration corridors had a significantly larger increase in wetland availability than species with longer and narrower migration corridors ($\beta = 0.016$, $t = 2.50$, $P = 0.01$). Similarly, the wetlands were less fragmented and isolated at higher latitude (GLM for wetland fragmentation, $\beta = 0.007$, $t = 17.64$, $DF =$

Table 2 Results of the logistic regressions of environmental factors on species presence for eight waterfowl species, showing the performance of the best models and regression coefficients (coefficient) for environmental factors included the best models

Model	Coefficient	SE	z-value	*p* value
Greylag goose (N = 178, AIC = 162.2, ΔAIC = 1.7, accuracy = 76.4%)				
(Intercept)	− 3.385	1.325	− 2.556	0.011*
Lake area [log(km^2)]	1.137	0.252	4.516	< 0.001***
Grass and crop resources [log(km^2)]	0.520	0.407	1.276	0.202
x	− 0.001	0.0002	− 5.088	< 0.001***
Swan goose (N = 114, AIC = 438.4, ΔAIC = 2.2, accuracy = 72.8%)				
(Intercept)	− 1.216	0.656	− 1.854	0.064
Lake area [log(km^2)]	0.822	0.146	5.628	< 0.001***
Grass and crop resources [log(km^2)]	0.399	0.198	2.022	0.043*
X	− 3.628e−04	1.348e−04	− 2.692	0.007**
x^2	− 6.455e−07	1.159e−07	− 5.570	< 0.001***
Bean goose (N = 394, AIC = 400.7, ΔAIC = 1.0, accuracy = 68.5%)				
(Intercept)	− 3.841	1.108	− 3.467	< 0.001***
Lake area [log(km^2)]	0.374	0.369	2.222	0.026*
Grass and crop resources [log(km^2)]	1.280	0.351	3.650	< 0.001***
x	1.472e−03	2.638e−04	5.579	< 0.001***
x^2	− 7.548e−07	1.715e−07	− 4.401	< 0.001***
Greater white-fronted goose (N = 714, AIC = 733.0, ΔAIC = 1.2, accuracy = 78.4%)				
(Intercept)	− 3.528	1.143	− 3.088	0.002**
Lake area [log(km^2)]	0.476	0.137	3.485	< 0.001***
Elevation [log(m)]	− 0.302	0.172	− 1.756	0.079
Grass and crop resources [log(km^2)]	1.383	0.333	4.153	< 0.001***
x	2.672e−03	3.004e−04	8.895	< 0.001***
x^2	− 1.513e−06	1.814e−07	− 8.342	< 0.001***
Lesser white-fronted goose (N = 114, AIC = 126.2, ΔAIC = 1.5, accuracy = 72.8%)				
(Intercept)	3.116	0.978	3.187	0.001**
Lake area [log(km^2)]	0.780	0.294	2.655	0.008**
Elevation [log(m)]	− 1.821	0.460	− 3.959	< 0.001***
x	4.268e−04	2.434e−04	1.753	0.080
Tundra swan (N = 446, AIC = 440.1, ΔAIC = 0.5, accuracy = 78.3%)				
(Intercept)	− 6.468	1.473	− 4.391	< 0.001***
Elevation [log(m)]	− 0.660	0.185	− 3.573	< 0.001***
Grass and crop resources [log(km^2)]	2.231	0.417	5.350	< 0.001***
x	1.741e−03	1.934e−04	9.008	< 0.001***
Common teal (N = 816, AIC = 893.0, ΔAIC = 1.0, accuracy = 75.5%)				
(Intercept)	− 1.979	0.614	− 3.222	0.001**
Lake area [log(km^2)]	0.562	0.103	5.446	< 0.001***
Grass and crop resources [log(km^2)]	0.470	0.194	2.425	0.015*
x	1.187e−03	1.075e−04	11.046	< 0.001***
x^2	− 1.315e−07	7.755e−08	− 1.695	0.090
Northern pintail (N = 2186, AIC = 1873.4, ΔAIC = 0.9, accuracy = 81.0%)				
(Intercept)	− 2.704	0.558	− 4.846	< 0.001***
Lake area [log(km^2)]	0.298	0.079	3.748	< 0.001***
Elevation [log(m)]	− 0.253	0.096	− 2.640	0.008**

Table 2 continued

Model	Coefficient	SE	z-value	*p* value
Grass and crop resources [log(km^2)]	0.647	0.154	4.211	< 0.001***
x	1.669e−03	1.044e−04	15.997	< 0.001***
x^2	1.252e−07	7.163e−08	1.748	0.080

ΔAIC is the difference between the AIC values of the best model and the second-best model (Appendix S2). Grass and crop resources were measured by the area of grasslands and croplands within the 32.5-km buffer surrounding each lake; *x* = centre *x* coordinate of each lake under the azimuthal equidistant projection. "***", "**", "*", "'" means the estimated regression coefficient was significant at 0.001 level, 0.01 level, 0.05, and 0.1 level, respectively

4619, $P < 0.01$; GLM for wetland isolation, $\beta = 0.009$, $t = 12.85$, $DF = 4619$, $P < 0.01$), and species with shorter and broader migration corridors had significantly less habitat fragmentation and isolation than species with longer and narrower migration corridors ($\beta = 0.088$, $t = 8.31$, $P < 0.01$; $\beta = 0.049$, $t = 2.77$, $P = 0.01$). Although wetland area for species with longer and narrower migration corridors increased at higher latitudes, that for species with shorter and broader migration corridors and a more western distribution increased more between 30 N–50 N in the areas of the Upper Yellow River and Mongolia (Fig. 3).

Discussion

The seasonal distributions of migratory waterfowl species determine the extent to which they are exposed to habitat degradation, which varies from place to place. As for migratory waterfowl in the East Asian–Australasian Flyway, habitat availability simultaneously degraded in the southeastern part of the flyway, i.e., in the coastal regions in China and Japan, but improved in inland regions of the western part of flyway (Fig. 2). Species with longer and narrower migration corridors that concentrate their migrations along the eastern coast could benefit less from improved habitat conditions in the southern part of their migration flyway compared to those with shorter and broader migration corridors. However, species with longer and narrower migration corridors could reach improved habitat conditions in Russia, in the northern part of their distribution range.

Areas of grassland and wetland in the suitable wetland sites in southern and eastern China and Japan decreased from 1992 to 2012 (Fig. 2b and c), and those areas could become spatial bottlenecks for species with main stopovers in these regions. Migratory species with spatial bottlenecks in degraded regions could be less resilient to habitat changes because of limited alternatives (Berger et al. 2008; Sawyer et al. 2009). These species must either skip the degraded wetlands or accept suboptimal conditions (Weber et al. 1999), leading to increased costs of migration, and consequently increased mortality during migration, and probably reduced efficiency of energy intake and reproduction. It could be difficult for the species experiencing successive habitat loss while migrating from their non-breeding to breeding grounds to replenish energy stores and maintain optimal body reserves for reproduction.

By investigating patterns of habitat change at the flyway scale, we further highlight the relationship between migratory extent and species-specific effects of environmental changes. Previous studies have found that migratory extent can affect species resilience to environmental changes. Species with a longer migration distance (Sanderson et al. 2006; Morrison et al. 2013), a smaller non-breeding area compared to breeding area (Gilroy et al. 2016), and a larger reliance on specific regions (e.g., South America and Yellow Sea tidal mudflat) are more vulnerable compared to others (North American Bird Conservation Initiative 2012; Studds et al. 2017). These facts can be explained when we relate their distributions to spatial patterns of habitat degradation at a flyway scale. Species occupying broader extent with more parallel alternative sites have plasticity in their reaction to habitat degradation. Species with shorter and broader migration corridors migrate across both degraded landscapes in the east and areas that have increased habitat availability in the west of the flyway. Despite the shorter migration distance of these species compared to the other study species, their migratory dispersion (i.e., larger non-breeding range size relative

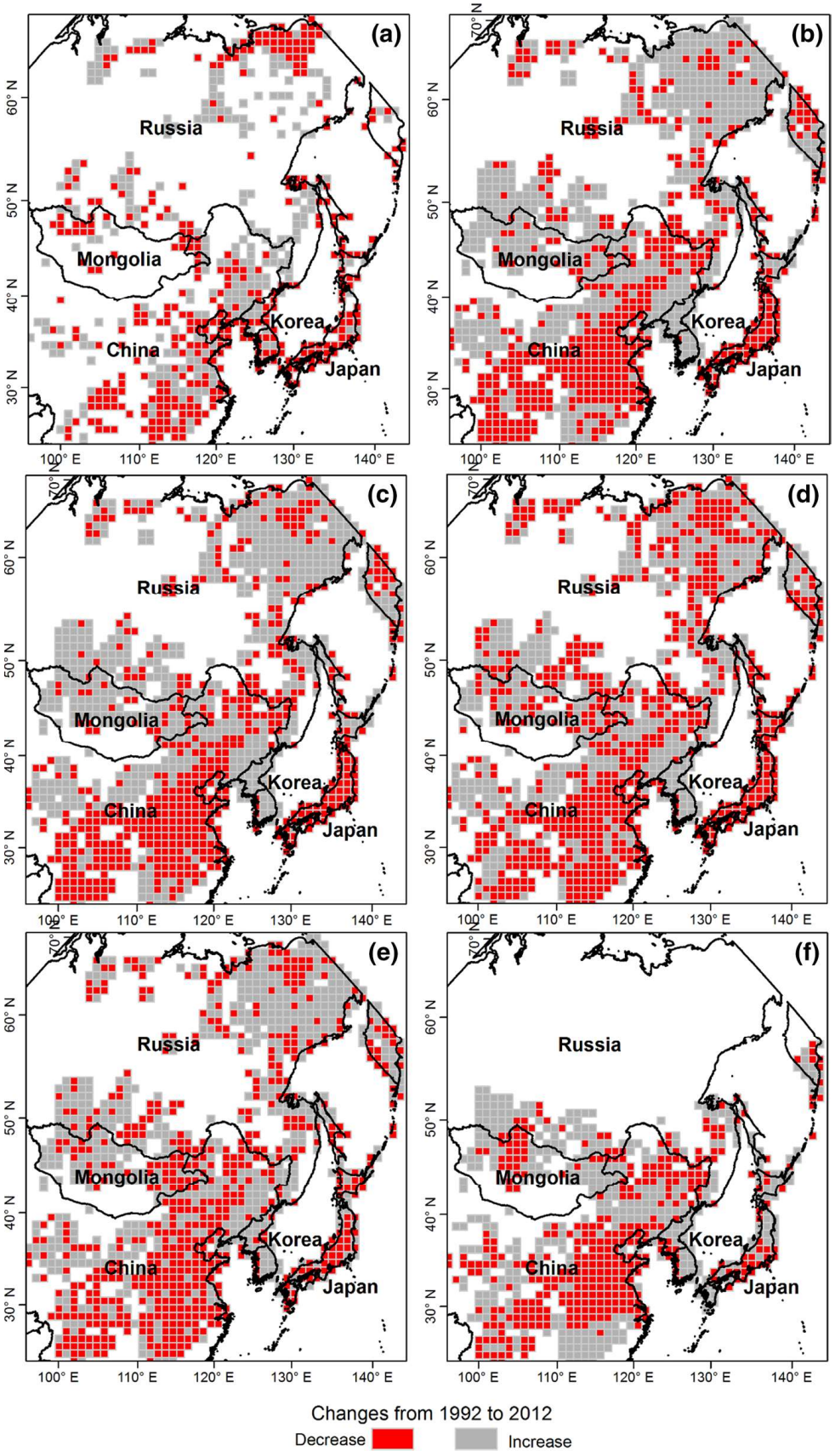

Fig. 2 Spatial patterns in changes in landscape metrics from 1992 to 2012. **a** Water loss as measured by the change in total water area; **b** grassland loss as measured by the change in total grassland area. **c** Wetland availability as measured by the change in the total wetland area; **d** wetland fragmentation as measured by the change in the mean patch area of wetlands; **e** Wetland isolation as indexed by the change in the Proximity Index of wetland patches; **f** changes in agriculture resources as measured by the change in the total cropland area. A negative value indicates a decrease in corresponding landscape metrics

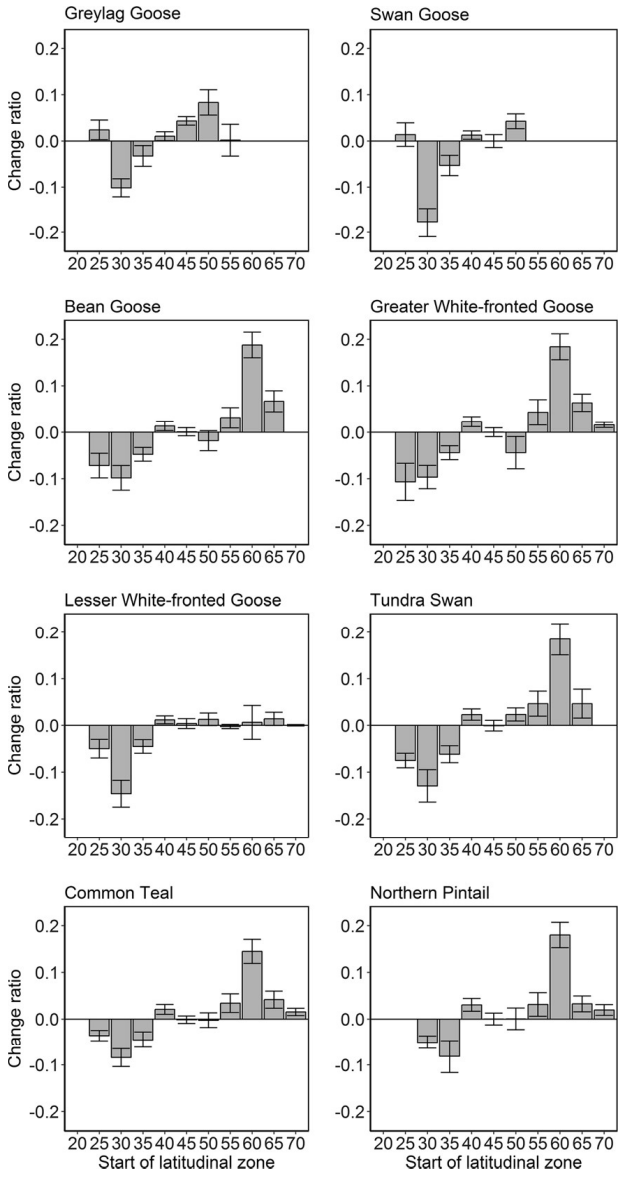

Fig. 3 Latitudinal patterns of change ratio (mean ± SD) of wetland availability (water surface and surrounding grasslands) in the suitable wetland sites from 1992 to 2012; x-axis represents five-degree latitudinal zones. A negative value indicates a decrease in area of wetlands in the corresponding latitudinal zone while a positive valued indicates an increase

to breeding) influences their resilience to habitat degradation. GPS tracking data also have shown that the swan geese from Mongolia migrate over a broad front, using a parallel configuration of stopover sites, although these geese share the same non-breeding and breeding grounds (Batbayar 2013). Swan geese can use stopover sites located at the western part of their flyway, where habitat degradation of stopover sites is lower than in the eastern part.

The wetlands of the East Asian–Australasian Flyway have been threatened by habitat loss, fragmentation, and isolation over the past two decades, which can subsequently impact migratory waterfowl by depleting resources and isolating wetland sites. Wetland degradation in eastern China and Japan contributed most to habitat destruction in the flyway from 1992 to 2012, partly as a consequence of rapid urbanization and socioeconomic development in East Asian countries since 1992 (Seto and Fragkias 2005). Wetlands on their non-breeding grounds with intensive human activities lost much of their area, triggering a human–wildlife conflict in which birds and people compete for resources (Fox et al. 2016; Jia et al. 2018). China has made rapid economic development since the economic reform in 1978, which is accompanied by accelerating environmental degradation, e.g., decreasing wetland area (Liu and Diamond 2005). Agricultural expansion is one of the most important threats to wetlands by forms of wetland conversion or water drainage for irrigation (Liu and Diamond 2005; Niu et al. 2012), and pollution and insufficient funding for protection are other contributing factors to wetland degradation (Liu and Diamond 2005). The coastal regions are confronted with larger problems compared to inland areas because of increased human pressure and sea-level rise, e.g., a considerable part of Japanese wetlands is threatened (Nicholls 2004; de Boer et al. 2011; Iwamura et al. 2013). On the contrary, natural habitats have recovered in the temperate zones of Russia due to a low human density and a widespread land abandonment since the sweeping reorganization of the Russian agriculture in 1990s (Grishchenko and Prins 2016).

Natural grasslands, as the primary foraging areas for waterfowl, are vulnerable because they are more sensitive to climate change than most human land-use types (Li et al. 2017c). Agriculture expanded around most wetlands and increased food resources for waterfowl, according to our modelling. For example, some wetlands in southeastern China are efficiently cultivated with multiple rice farming systems (Li et al. 2017a). However, these benefits might be a trade-off against greater human disturbance around these wetlands and increased wetland loss to land reclamation. Farmlands reclaimed in or around lakes and wetlands, sacrifice roosting and primary foraging sites (e.g., recessional grasslands) of waterfowl. Thus, waterfowl species are also more confined to their natural habitats

instead of exploiting surrounding farmlands in their non-breeding grounds, and they tend to select habitats with lower human pressures in China (Yu et al. 2017; Li et al. 2017b). Moreover, there are other forms of habitat degradation for migratory waterfowl which have not been measured by the metrics quantified in our study, but can decrease waterfowl species diversity and reduce wetland quality, e.g., pollution with pesticides and heavy metals, changes in water levels by dams, poaching and hunting activities, and low efficiency of local conservation regulations (MaMing et al. 2012; Aharon-Rotman et al. 2017). In the future, ecological restoration projects considering these factors might offer some potential (An et al. 2007; Li et al. 2015) to conserve critical wetlands in the Middle and Lower Yangtze River, Lower Yellow River, and Japan.

Wetland degradation poses severe challenges to migratory species because wetland loss can reduce local abundance and species richness (Mora et al. 2011). Considering each wetland patch as an island surrounded by suboptimal or unsuitable habitats, both the loss of wetland area and isolation from other wetlands can trigger local extinction of populations (MacArthur and Wilson 1967; Purvis et al. 2000). The vulnerability of a population increases when even only a part of the migration network across a large spatial extent is affected (Iwamura et al. 2013). The population decline of migratory birds in relation to habitat degradation in the East Asian–Australasian Flyway has therefore triggered concern (Syroechkovskiy 2006; Cao et al. 2010; Sutherland et al. 2012), as East Asian populations of bean goose, greater white-fronted goose, lesser white-fronted goose, common teal, swan goose, and northern pintail are generally decreasing (Syroechkovskiy 2006; Cao et al. 2010; Wetland International 2017). Previous studies have suggested that a couple of bottleneck sites in their migration network explain these population declines. For example, the Yellow Sea tidal mudflat has shrunk by more than 65%, and consequently, the migratory shorebirds that highly rely on the Yellow Sea tidal mudflat experienced large population declines (Studds et al. 2017). The effect of habitat degradation on population size, especially for those species that use multiple stopover sites, depends not only on the overall extent of habitat degradation (Rogers et al. 2010; Iwamura et al. 2013), but also on where this degradation occurs (Runge et al. 2014). Our results demonstrate that habitat degradation in the migration flyway has a strong spatial component, which may explain differences in the population dynamics of migratory waterfowl species.

Because migratory species might be able to respond to habitat degradation by altering migration routes, future studies should focus on both specific regions and on the integrity of the whole migration network and on the plasticity of the species in terms of migratory movements and visited stopover sites. Hence, a network approach is required to better understand changes in migration strategy and population dynamics of migratory species. Remote-sensing techniques and temporal land cover data allow us to monitor the environmental changes at flyway scale (Si et al. 2015). There is, therefore, a demand for higher-accuracy and finer-resolution land cover datasets to support studies on the large-scale environmental changes in the framework of migration and conservation biology.

Conclusion

This study relates species seasonal distribution to species-dependent effects of habitat degradation in the migratory flyway. We have demonstrated that eight waterfowl species in the East Asian–Australasian Flyway are all exposed to habitat degradation in their non-breeding areas, but that conditions around wetland sites improve with increasing latitudes. Comparing changes at the same latitude, wetland sites for species with longer and narrower migration corridors degraded more from 1992 to 2012 than for species with shorter and broader migration. We conclude that migratory species with narrower distributions and longer migration distances are exposed to a higher level of habitat degradation because they have fewer parallel sites to provide alternative stopover, roosting, or foraging sites when habitat is degraded or lost. Hence, selection of important conservation regions for migratory birds should not only depend on local conditions of wetland sites but also take species-specific seasonal distributions into account. Especially, more efforts should be targeted along the migration routes of species with a narrow seasonal distribution and spatial bottlenecks in degraded regions of the flyway. Moreover, it is necessary to limit reclamation of wetland resources and

unrestrained water drainage in regions of the East Asian–Australasian Flyway because wetlands in the Middle and Lower Yangtze River, Lower Yellow River, and Japan are major non-breeding grounds as well as important stopover areas for many waterbird species.

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Appendix E

China's wintering geese can thrive by reducing human pressure on farmland

Reducing human pressure on farmland could rescue China's declining wintering geese

Yali Si[1,2,3*], Jie Wei[1], Wenzhao Wu[1], Wenyuan Zhang[1,4], Lin Hou[5], Le Yu[1] and Ben Wielstra[6,7]

Abstract

Background: While goose populations worldwide benefit from food provided by farmland, China's threatened wintering goose populations have failed to capitalize on farmland. It has been proposed that, due to an exceptionally intense human pressure on Chinese farmland, geese cannot exploit farmland in their wintering sites and hence are confined to their deteriorating natural habitat. If this were true, locally decreasing this human pressure on farmland 'refuges' would represent a promising conservation measure.

Methods: We investigate habitat use of two declining migratory goose species in their core wintering (Yangtze River Floodplain) and stopover (Northeast China Plain) regions, compare the human pressure level at both regions, and adopt a mixed-effect resource selection function model to test how human pressure, food resource type (farmland or wetland/grass), distance to roosts, and their interaction terms influence the utilization of food resources for each species and region. To this aim we use satellite tracking of 28 tundra bean geese *Anser serrirostris* and 55 greater white-fronted geese *A. albifrons*, a newly produced 30 m land cover map, and the terrestrial human footprint map.

Results: Geese use farmland intensively at their stopover site, but hardly at their wintering site, though both regions have farmland available at a similar proportion. The human pressure on both farmland and wetland/grass is significantly lower at the stopover region compared to the wintering region. At both sites, the two goose species actively select for farmland and/or wetland/grass with a relatively low human pressure, positioned relatively close to their roosting sites.

Conclusions: Our findings suggest that if human pressure were to decrease in the farmlands close to the roost, China's wintering geese could benefit from farmland. We recommend setting aside farmland near roosting sites that already experiences a relatively low human pressure as goose refuges, and adopt measures to further reduce human pressure and increase food quality and quantity, to help counter the decline of China's wintering goose populations. Our study has important conservation implications and offers a practical measure for migratory waterfowl conservation in areas of high human-wildlife conflict.

Keywords: Yangtze River floodplain, Northeast China plain, Satellite tracking, Habitat use, Refuge, Alternative feeding area, Agricultural land, Resource selection function model

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Background

Chinese wintering geese have rapidly declined [1]. While wintering goose populations have benefited from the increased food supply provided by agricultural land across most of the Northern Hemisphere [2, 3], this appears not to be the case in China. It has been proposed that, due to the exceptionally intense human pressure on China's farmland, the goose populations wintering in China cannot exploit the riches provided by agricultural land and hence geese are 'imprisoned' here inside their degrading natural habitat [4]. In general, geese respond negatively to human disturbance as a net loss in energy stores, resulting from a decreased intake and an increased expenditure related to avoidance behavior, which reduces migration and breeding success [5, 6].

The corollary is that, if human pressure on farmland were to decrease, geese in China could take advantage of farmland. This would have important conservation implications because 'refuges' – patches of farmland where human pressure is reduced as they are temporarily set aside as alternative feeding area for birds – have shown to boost goose populations in other parts of the world [3, 7–11]. If it can be shown that Chinese wintering geese do venture into farmland in regions where human pressure is lower, this would demonstrate that these geese are likely to benefit from the creation of farmland refuges in their wintering site.

We test our prediction by taking advantage of the fact that human pressure on farmland shows spatial variation across China [12, 13]. To this aim, we use satellite tracking data (Fig. 1) of tundra bean geese (*Anser serrirostris*; $n = 28$) and greater white-fronted geese (*A. albifrons*; $n = 55$) that winter in the Yangtze River Floodplain and use the Northeast China Plain as a core stopover site, during

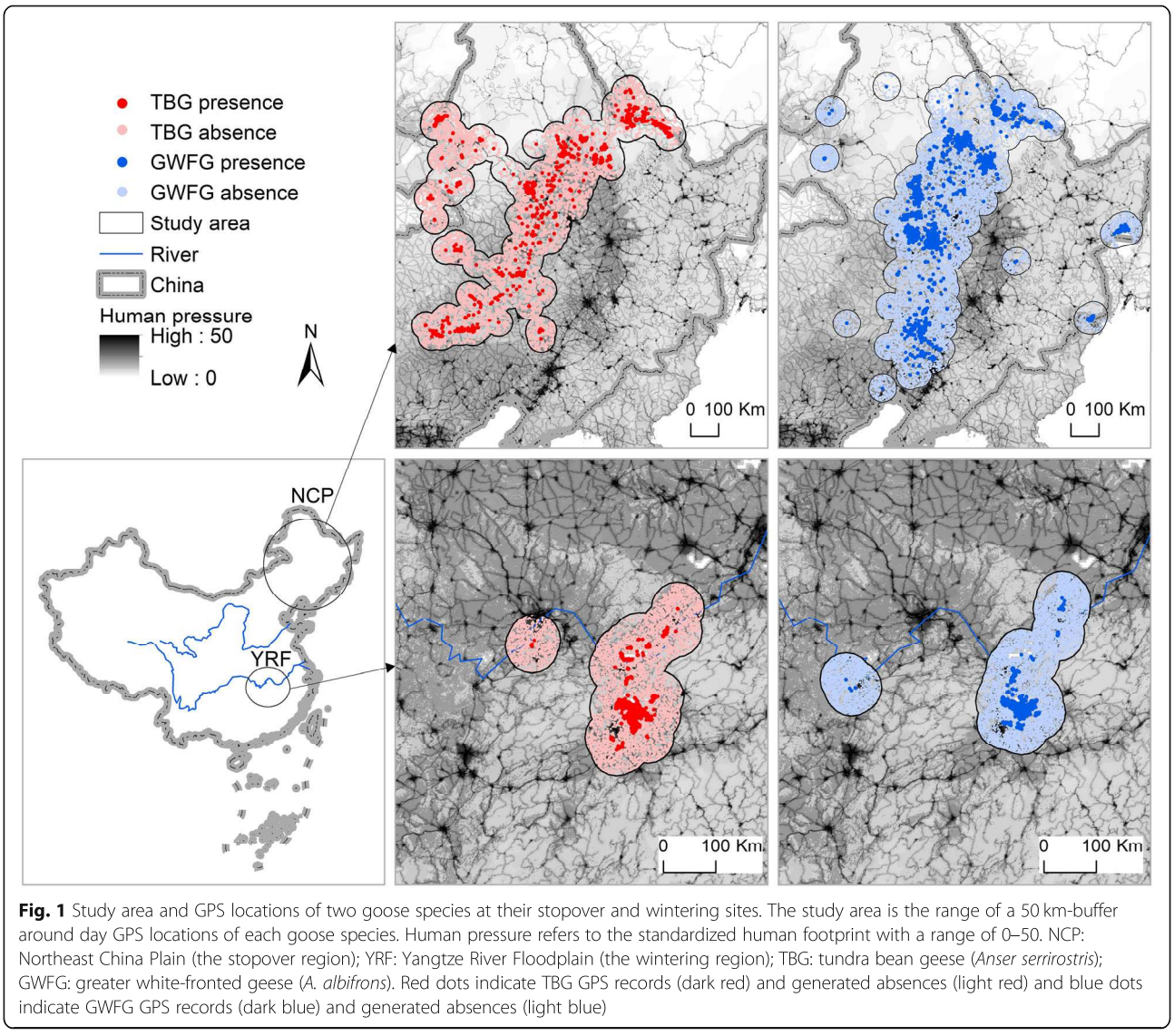

Fig. 1 Study area and GPS locations of two goose species at their stopover and wintering sites. The study area is the range of a 50 km-buffer around day GPS locations of each goose species. Human pressure refers to the standardized human footprint with a range of 0–50. NCP: Northeast China Plain (the stopover region); YRF: Yangtze River Floodplain (the wintering region); TBG: tundra bean geese (*Anser serrirostris*); GWFG: greater white-fronted geese (*A. albifrons*). Red dots indicate TBG GPS records (dark red) and generated absences (light red) and blue dots indicate GWFG GPS records (dark blue) and generated absences (light blue)

their migration to and from the Arctic breeding sites [14]. As a proxy for human disturbance on farmland, we adopt the recently published Global Terrestrial Human Footprint Map, a cumulative human footprint measure based on infrastructure, land cover and human access into natural areas [12, 13].

For both goose species we 1) compare the human pressure between the wintering and the stopover region and 2) investigate habitat use at both the wintering and the stopover region. Furthermore, we 3) test whether geese actively select for resources with a relatively low human pressure, by building a mixed-effect resource selection model using human pressure, resource types (farmland and wetland/grass), distance to roosts, and their interaction terms as fixed factors, and year and individual as random factors.

Materials and methods

Tracking data

Geese were captured at Poyang Lake in the Yangtze River Floodplain, Jiangxi Province, China (29°N, 116°E) during the 2014-2018 wintering seasons, and equipped with GPS - GSM (Global Positioning System - Global System for Mobile Communications), solar- powered loggers. Further background on capture and deployment methods can be found in Si et al. [14]. Each logger was set to record GPS (Global Position System) positions every 2 h. The collected data used in this study include bird ID, latitude and longitude (degree), time of record, and speed (km/hour). We used tracking data from 28 individuals of tundra bean goose and 55 individuals of greater white-fronted goose for further analyses.

The start and end dates of wintering / spring staging in the Yangtze River Floodplain and stopover in the Northeast China Plain for each individual were defined as the first day it arrived/left the specific site and showing continuous presence/absence. For individuals with multi-year data, the year with the highest amount of GPS records was used. Records with a GPS location error over 30 m and/or speed over 1 km/hour (presumably while in flight instead of foraging) were removed from downstream analyses. The sunrise and sunset time were calculated based on the geographic location of each GPS record using algorithms provided by the National Oceanic & Atmospheric Administration (NOAA) (https://www.esrl.noaa.gov/gmd/grad/solcalc/). Day and night locations were defined as the locations recorded in the periods between 1 h before sunrise to 1 h after sunset, and 1 h after sunset to 1 h before sunrise. For each individual bird, day and night counts of locations, start and end dates at the wintering and stopover region, and logger information are summarized in Additional file 1: Table S1.

Habitat use at both regions

We produced a 2015 China land cover map at a 30 m resolution according to Liu et al. [15] with an overall accuracy over 91% and used this to compare the habitat use of tracked geese at their wintering and stopover regions. Land cover types were regrouped to farmland, woodland, grassland, water, wetland (i.e., swamp, mud flat and bottomland), built-up land, and bare land (i.e., sand, desert, saline-alkali land and bare land). To compare the use of different food resources, land cover types were regrouped and the percentage of tracked locations during the day and at night on farmland, water/wetland/grass (grassland are included to cover wet meadows), and others (the rest land cover types) was calculated in both the wintering and the stopover region.

Compare human pressure on habitats in both regions

For each species, we defined the study area as the range of a 50 km buffer around the GPS locations of a specific species recorded during the day at their wintering or stopover region (Fig. 1). We chose 50 km because the maximum foraging flight distance for American and European geese are generally smaller than this [8, 16, 17], and hence both used and unused area should be included. We then compared the human pressure on habitats for each species at each region. The 2009 Global Terrestrial Human Footprint Map with a 1 km resolution [13] was used to extract the human pressure on farmland and wetland/grass located within the study area of each bird species in both the wintering and the stopover region. This standardized human footprint map (with a range of 0–50) was generated by integrating remotely sensed and bottom-up survey information that measure direct and indirect human pressures on the environment, including data on the extent of built environments, crop land, pasture land, human population density, night-time lights, roads, railways, and navigable waterways. To test whether human pressure differs between the wintering and stopover region, a Mann-Whitney U test was conducted, as the data were not normally distributed.

Resource selection function modelling

We tested if geese actively select farmland and wetland/grass close to their roosting area and with a relatively low human pressure, using mixed-effect resource selection function modelling. For each region, within the study area of each species, we used daytime GPS records located on farmland and wetland/grass as presence, and randomly generated an equal number of absences on these two land cover types in the part of the study area where geese were not present (Fig. 1). The minimum distance between an absence point and its closest presence point was set to 1 km. To take the resource availability into account, the number of absences generated

on each food resource type was calculated based on the farmland and wetland/grass composition in the study area of each species in each region (tundra bean geese in the Northeast China Plain: 48, 51%; greater white-fronted geese in the Northeast China Plain: 66, 34%; tundra bean geese in the Yangtze River Floodplain: 84, 16%; greater white-fronted geese in the Yangtze River Floodplain: 82, 18%). For each species on each day, the distance to the roost was calculated as the distance from a specific GPS point recorded during the day to the center location of GPS points recorded in the previous night. We then built a mixed-effect resource selection function model [18], estimated by the generalized linear mixed model with a logit link, to predict bird presence for each species at each region separately. Specifically, we used human pressure, food resource (land cover) type (farmland and wetland/grass, with farmland as the baseline), distance to roosts, and their interaction terms as the fixed factors, and bird ID and year as random factors. As we mainly focused on the fixed effects, the Akaike information criterion (AIC) was used to rank the top fixed-effect model first, and random factors were added afterwards. Response curves of factors with a significant effect on bird presence were constructed by fixing all variables other than the variable of interest constant at their median values, and making predictions at regular intervals over the range of the given variable. The response curves of the interaction terms were calculated by fixing all variables other than the two independent factors (1 and 2) in the specific interaction term constant at their median values, and making predictions for factor 1 at regular intervals over the non-outlier range of factor 2. To facilitate comparing among models, we also produced the predictions for factor 1 at a fixed value of factor 2 (e.g., with a fixed distance to the roost). The 95% confidence interval (CI) was calculated using the Wald confidence interval based on the sampling distribution of the Wald statistic in repeated samples. Only the response curve of the interaction term was plotted if both the interaction and the single term were significant. Analyses were carried out in R 3.5.3 [19], using 'glmmTMB' and 'effects' packages.

Results

The composition of farmland in the study area of each species in the Northeast China Plain (tundra bean geese = 38%, greater white-fronted geese = 49%) and the Yangtze River Floodplain (tundra bean geese = 45%, greater white-fronted geese = 46%) is similar (Fig. 2). Both goose species mostly stick to their natural habitat

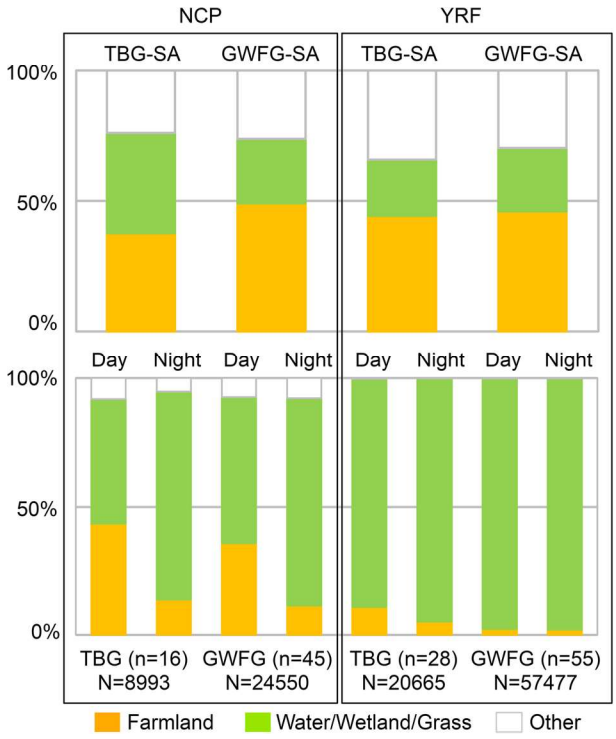

Fig. 2 Land cover composition of the study area (above) and habitat use of tracked geese (below). NCP: Northeast China Plain (the stopover region); YRF: Yangtze River Floodplain (the wintering region); TBG tundra bean geese (*Anser serrirostris*); GWFG: greater white-fronted geese (*A. albifrons*); SA: study area (see Fig. 1). Habitat use is quantified by the percentage of GPS locations on specific land cover types. n: number of tracked individuals; N: number of GPS locations

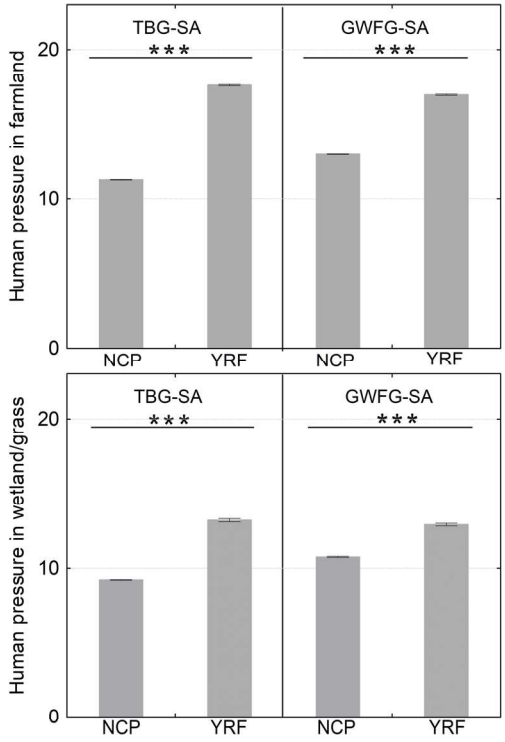

Fig. 3 Human pressure on farmland and wetland/grass in the study area. Human pressure refers to the standardized human footprint with a range of 0–50. NCP: Northeast China Plain (the stopover region); YRF: Yangtze River Floodplain (the wintering region); TBG tundra bean geese (*Anser serrirostris*); GWFG: greater white-fronted geese (*A. albifrons*); SA: study area (see Fig. 1). Asterisks indicate a significant difference in human pressure; error bars are 95% confidence intervals around the mean

in the wintering site Yangtze River Floodplain, with 90% (tundra bean geese) and 98% (greater white-fronted geese) of GPS records during the day located in water/wetland/grass (Fig. 2). In contrast, we show that both goose species do intensively exploit farmland in the stopover site Northeast China Plain, with 44% (tundra bean geese) and 36% (greater white-fronted geese) of GPS records during the day located on farmland (Fig. 2).

According to the Mann-Whitney U test, human pressure on farmland and wetland/grass in the study area of both goose species is significantly lower in the stopover site Northeast China Plain than in the wintering site Yangtze River Floodplain (Fig. 3; Table 1). We find that roost distance and human pressure show a pronounced effect (individually and/or as an interaction term) on bird presence, suggesting that geese actively select for farmland and/or wetland/grass that is under a lower human pressure and located close to their roosts (Fig. 4a, c, e, f, h, and i; Table 2; Additional file 1: Fig. S1). Both species prefer wetland/grass over farmland, except for

Table 1 Summary of Mann-Whitney U test comparing human pressure level in different regions

Species	Land cover type	Location	Mean	95% CIs	N	U	*p*
TBG	Farmland	YRF	17.593	17.548–17.638	50,278	1.53E+ 10	< 0.001
		NCP	11.286	11.267–11.304	372,100		
	Wetland/grass	YRF	13.174	13.069–13.279	10,456	2.96E+ 9	< 0.001
		NCP	9.146	9.131–9.160	390,058		
GWFG	Farmland	YRF	16.955	16.913–16.998	45,441	1.67E+ 10	< 0.001
		NCP	12.814	12.797–12.831	492,559		
	Wetland/grass	YRF	12.881	12.790–12.972	11,253	1.93E+ 8	< 0.001
		NCP	9.824	9.804–9.845	252,385		

The Northeast China Plain (NPC) stopover site has a significantly lower level of human pressure on the farmland and wetland/grass, in comparison to the Yangtze River Floodplain (YRF) wintering site. Human pressure refers to the standardized human footprint with a range of 0–50. TBG: tundra bean goose (*Anser serrirostris*); GWFG: greater white-fronted goose (*A. albifrons*). CIs: confidence intervals; N: sample size

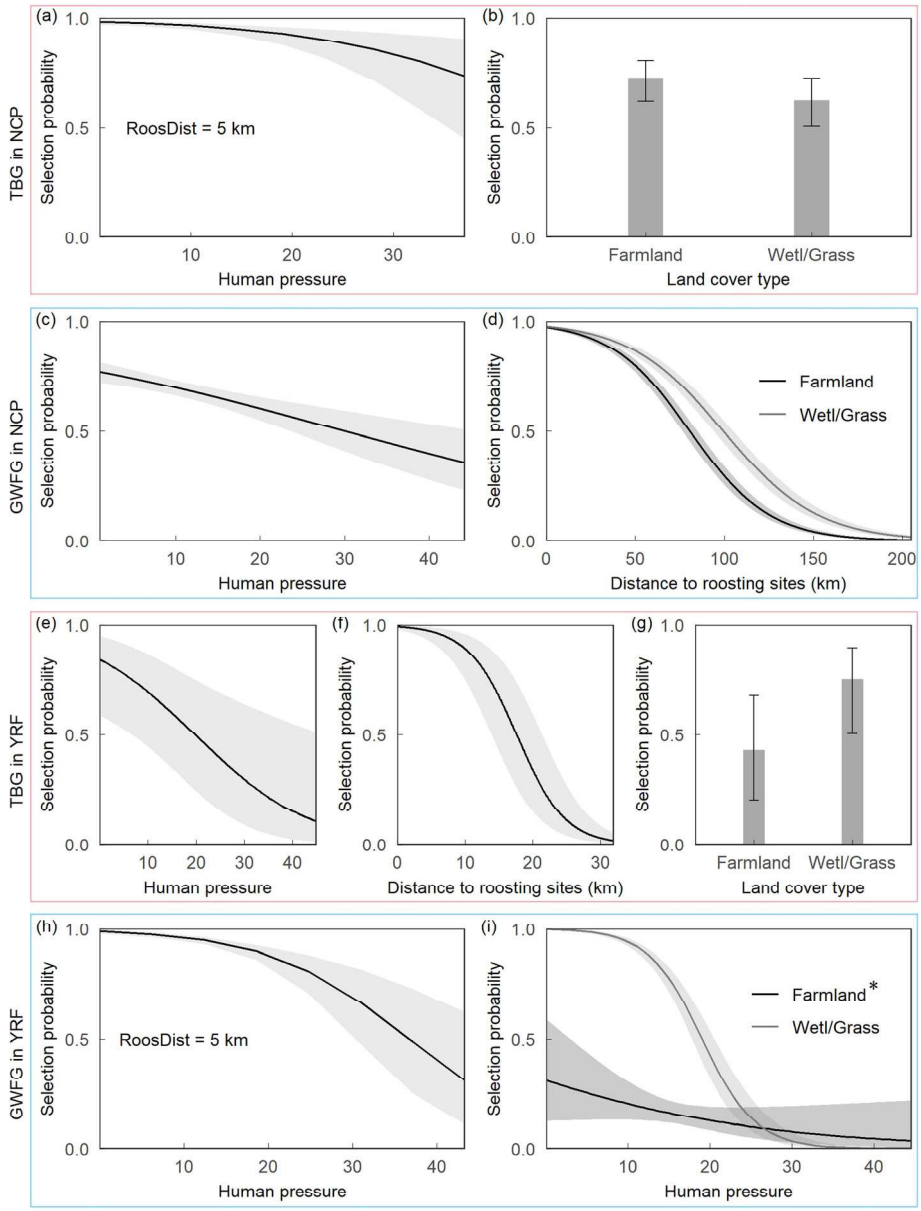

Fig. 4 Geese select farmland and wetland/grass near their roosts and experiences relatively low human pressure. Lines indicate response curves, and grey areas and bars 95% confidence intervals. Human pressure refers to the standardized human footprint with a range of 0–50. **a**-**b**: tundra bean geese (*Anser serrirostris*, TBG) in the stopover region Northeast China Plain (NCP); **c**-**d**: greater white-fronted geese (*A. albifrons*, GWFG) in NCP; **e**-**g**: TBG in the wintering region Yangtze River Floodplain (YRF); **h**-**i**: GWFG in YRF. RoostDist: distance to roosting sites; Wetl/Grass: wetland and grass; *: the relatively low selection probability reflects extrapolation beyond the actual level of human pressure (mean = 17.04 and standard deviation = 4.37) based on the relatively little geese presences on farmland

tundra bean geese show a higher preference for farmland at the Northeast China Plain (Fig. 4b and g, Table 2).

Discussion

We demonstrate that China's wintering geese can and do venture outside of their threatened natural habitat, in order to exploit the resources offered by farmland, but only under the condition that human pressure is low and the farmland is in close proximity to roosting sites. In the absence of good quality natural habitat during the wintering period, it is critical that geese are able to access the resources provided by farmland, so that sufficient energy can be stored to successfully undertake migration and breeding. Our findings underline that wintering geese seldom exploit farmland in the Yangtze

Table 2 Summary of the top resource selection function model quantifying the environmental effect on goose presence

	NCP				YRF			
	TBG		GWFG		TBG		GWFG	
Fixed effects	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Intercept	−5.36	0.324***	−5.77	0.197***	−14.03	0.828***	−14.78	0.421***
HP	0.35	0.189	−0.21	0.047***	−0.45	0.165**	−3.06	0.643***
RoostDist (km)	−10.83	0.360***	−11.50	0.289***	−22.42	0.937***	−22.43	0.589***
LC	−0.43	0.136**	1.61	0.255***	1.39	0.262***	3.48	0.200***
HP*RoostDist	1.03	0.299***	–	–	–	–	−4.57	0.929***
HP*LC	0.24	0.130	–	–	–	–	−1.54	0.230***
RoostDist*LC	–	–	1.80	0.409***	–	–	–	–
Random effects	Variance	SD	Variance	SD	Variance	SD	Variance	SD
BirdID	0.130	0.361	0.221	0.470	0.977	0.988.	0.390	0.624
Year	0.100	0.317	4.94E-9	7.03E-5	0.848	0.921	0.030	0.172

NCP Northeast China Plain, *YRF* Yangtze River Floodplain, *TBG* tundra bean goose (*Anser serrirostris*), *GWFG* greater white-fronted goose (*A. albifrons*), *HP* human pressure (refers to the standardized human footprint with a range of 0–50), *RoostDist* distance to the roost, *LC* land cover type (farmland and wetland/grass, with farmland as the baseline), *BirdID* bird individual ID, *SE* standard error, *SD* standard deviation, – no value as the variable is not selected in the best model
***: $P < 0.001$; **: $P < 0.01$; *: $P < 0.05$

River Floodplain, presumably due to the high level of human pressure on the farmland in this region.

The intensity of human activities is the main factor explaining the difference in use of farmland in the Yangtze River Floodplain wintering site and the Northeast China Plain stopover site. The wintering site is a highly populated area, with human settlements positioned much closer to natural wetlands and surrounding farmlands than in the stopover site. In the stopover site, tundra bean geese prefer farmland over wetland/grass, mainly due to the relatively lower level of human pressure in the farmland, as well as avoiding the competition with greater white-fronted geese, which favor wetland meadows over farmland [20].

Given that habitat loss is identified as the top threat to Chinese wintering waterbirds [21], not being able to explore alternative farmland food resources in the core wintering region likely contributed to the considerable population reduction of Chinese wintering geese. Setting aside farmland refuges, especially at the heavily disturbed key wintering site, the Yangtze River Floodplain, is a promising conservation measure for China's wintering geese. The Yangtze River Floodplain is one of the most important freshwater ecoregions in the world, containing an exceptional range of biodiversity and environmental conditions [22]. However, this area is also under severe environmental pressure, due to habitat loss, changes in the hydrological regime, pollution and overexploitation [23]. Hence, concrete conservation plans to safeguard this unique ecosystem are particularly urgent. Regarding the Northeast China Plain stopover site, while the current human pressure level allows birds to use farmland to a certain degree, setting farmland refuges would be an effective way to avoid future habitat deterioration.

Allocating part of the total farmland surface as refuges is a tried-and-tested approach that both improves geese survival and reduces goose-agriculture conflicts [10, 11, 24]. Effective design of a refuge network should consider both the selection of suitable farmland patches and improvement of the quality of the designated refuges by management. Furthermore, a compensation scheme for farmers that contribute part of their land to the refuge network needs to be implemented [24].

For the selection of suitable farmland, we suggest using our findings as the primary guideline, to identify suitable farmlands that 1) already experience a relatively low human pressure and 2) are in the close proximity to roosting sites. Furthermore, historic use could be considered to further prioritize suitable farmlands [25]. Food quality and quantity critically influence habitat use [8, 26] and could be used to further improve the selection procedure. In regards to refuge management, measures for minimizing human disturbance and increasing food quality and quantity should be adopted [11]. For the Yangtze River Floodplain wintering site, strict measures should be applied to lower the human disturbance in the designated farmlands, especially during the bird wintering season, such as rechanneling or limiting the use of the intersecting roads, lowering noise pollution (e.g., prohibiting the use of motor bikes and fireworks), and restricting human entry and activities. The food quality and quantity in refuges can be improved further by planting highly nutritious

food, or by leaving more grains in field and/or removing free-ranging poultry competing for food. For the Northeast China Plain stopover site, where human pressure is currently relatively low and birds can still use the farmland, measures preventing aggravation of the level of disturbance need to be applied to avoid future deterioration, i.e., changing farmland to built-up area or planning intensive development around the refuges. Lastly, a compensation scheme to farmers would stimulate the implementation of the above measures.

Conclusions

China's wintering geese could benefit from farmland if the human pressure on the farmland close to the roosts were to decrease. A network of refuges would open up an as yet practically untapped but abundant source of nutrition for China's wintering goose populations and could help counter their massive decline – as has already proven effective elsewhere around the world. We recommend that a pilot study is started as soon as possible. If done right, farmland refuges could offer a practical measure for migratory waterfowl conservation in areas of high human-wildlife conflict.

Supplementary information

Supplementary information accompanies this paper at https://doi.org/10.1186/s40462-020-00220-y.

Additional file 1: Figure S1. Geese select areas experiencing relatively low human pressure, at different distances to roosts. **Table S1.** Summary of GPS records obtained for 83 geese at their stopover and wintering regions.

Abbreviations

GPS: Global Positioning System; GSM: Global System for Mobile Communications; NOAA: The National Oceanic & Atmospheric Administration; AIC: Akaike information criterion; CI: Confidence Interval

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Authors' contributions

YS and BW conceived and designed the methodology; YS, JW, WZ and WW captured geese and attached loggers in the field; YS, JW, LH, WW, WZ and LY analyzed the data; YS and BW wrote the manuscript. All authors commented and approved the final version of the manuscript.

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Availability of data and materials

The dataset supporting the conclusions of this article is available in the Movebank Data repository (https://www.movebank.org) under ID 52997422, study '2015 Tsinghua waterfowl (Yangtze)'. For each individual bird, day and night counts of locations, start and end dates at the wintering and stopover site, and logger information are summarized in Additional file 1: Table S1.

Ethics approval and consent to participate

Capturing and deploying GPS transmitters on migratory birds was approved by the Jiangxi Provincial Forestry Bureau (reference number: Ganlinban 201514 and 201570) and the Animal Ethics Committee at Tsinghua University (reference number: IACUC15- SYL1).

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Appendix F

Habitat and surrounding matrices influence waterbird diversity

Multiscale effects of habitat and surrounding matrices on waterbird diversity in the Yangtze River Floodplain

Boyu Gao · Peng Gong · Wenyuan Zhang · Jun Yang · Yali Si

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Abstract

Context With the expansion in urbanization, understanding how biodiversity responds to the altered landscape becomes a major concern. Most studies focus on habitat effects on biodiversity, yet much less attention has been paid to surrounding landscape matrices and their joint effects.

Objective We investigated how habitat and landscape matrices affect waterbird diversity across scales in the Yangtze River Floodplain, a typical area with high biodiversity and severe human-wildlife conflict.

Methods The compositional and structural features of the landscape were calculated at fine and coarse scales. The ordinary least squares regression model was adopted, following a test showing no significant spatial autocorrelation in the spatial lag and spatial error models, to estimate the relationship between landscape metrics and waterbird diversity.

Results Well-connected grassland and shrub surrounded by isolated and regular-shaped developed area maintained higher waterbird diversity at fine scales. Regular-shaped developed area and cropland, irregular-shaped forest, and aggregated distribution of wetland and shrub positively affected waterbird diversity at coarse scales.

Conclusions Habitat and landscape matrices jointly affected waterbird diversity. Regular-shaped developed area facilitated higher waterbird diversity and showed the most pronounced effect at coarse scales. The conservation efforts should not only focus on habitat quality and capacity, but also habitat connectivity and complexity when formulating development plans. We suggest planners minimize the expansion of the developed area into critical habitats and leave buffers to maintain habitat connectivity and shape complexity to reduce the disturbance to birds. Our findings provide important insights and practical measures to protect biodiversity in human-dominated landscapes.

Keywords Biodiversity conservation · Waterbird habitat · The landscape matrix · Landscape

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connectivity · Shape complexity · Urban and rural planning

Introduction

Anthropogenic landscape modification is the major cause of biodiversity loss (Fischer and Lindenmayer 2007; Guadagnin and Maltchik 2007), and is one of the most pressing challenges for ecologists and conservation biologists. Globally, urban and rural areas are developing rapidly (Andrade et al. 2018), vastly altering the landscape composition and structure of wildlife habitats and their surroundings. However, the influence on urban development is not ubiquitous for biodiversity and is instead dependent on landscape composition and configuration at local and regional scales (Andrade et al. 2018). Wetlands, as important biodiversity hotspots, maintain high biodiversity and biological productivity (Forbes 2000; Dudgeon et al. 2006; Green et al. 2017), and offer habitat for many threatened species (Green 1996; Dudgeon et al. 2006). Though some wetlands are under protection, human activities remain a threat to wetland biodiversity, resulting in degraded ecosystem services (Green 1996; Nassauer 2004; Galewski et al. 2011; Martínez-Abraín et al. 2016). For example, due to dryland development, such as for agriculture and urban construction, large numbers of natural wetlands are deteriorated (Nilsson et al. 2005; Niu et al. 2012). Waterbirds (e.g. swans, geese, ducks, and herons), that rely on wetland habitats are sensitive to the environmental change and are often regarded as important indicators of ecosystem health (Ogden et al. 2014). Nevertheless, populations of such important bird groups are declining globally, which calls for new strategies for conservation of both waterbirds and wetlands (Amano et al. 2018).

Habitat characteristics influence bird distribution, abundance and diversity (Paracuellos and Telleria 2004; Beatty et al. 2014). For example, Zhang et al. (2018) found that waterfowl prefer areas with well-connected waterbodies and wetlands. Neotropical migrants are more abundant in landscapes with a greater proportion of forest and wetland (Flather and Sauer 1996). Shorebird abundance is positively affected by wetland area and number of wetlands (Webb et al. 2010). Moreover, greater habitat patch size, core area, edge and connectivity positively influence bird diversity (Wu et al. 2011). Nevertheless, the suitability of an area for birds depends on the condition of both habitat and the surrounding landscape matrix (Saab 1999; Guadagnin and Maltchik 2007; Elphick 2008; Perez-Garcia et al. 2014). For example, Morimoto et al. (2006) found that two woodland bird species prefer woodlands surrounded by agricultural areas over those surrounded by urban areas. Francesiaz et al. (2017) found that gulls prefer ponds surrounded by meadow and fallow land rather than woodland. Dallimer et al. (2010) found that the size of urban area and the amount of grassland patches affect the richness of moorland bird species in northern England. Nevertheless, studies investigating the effect of the landscape matrix have mainly considered the distance of the landscape matrix to habitats (Debinski et al. 2001; Summers et al. 2011), or the size and amount of the matrix (Guadagnin et al. 2009; Dallimer et al. 2010; Egerer et al. 2016). Thus, the effect of detailed characters (such as shape complexity and connectivity) of the surrounding landscape matrix on bird diversity are largely unknown.

Landscape metrics are frequently used to evaluate landscape pattern change (Riitters et al. 1995; Lausch and Herzog 2002), habitat characters (Mcalpine and Eyre 2002; Bailey et al. 2007), and linked to biodiversity (Bailey et al. 2007; Walz 2011; García-Llamas et al. 2018). Landscape metrics can be used to assess biodiversity at a higher and integrated level (Walz 2011) as higher environmental diversity leads to higher species diversity (Ricotta et al. 2003). These metrics can also capture biotic processes, such as immigration (Honnay et al. 2003) and biotic interactions (Simmonds et al. 2019). Numerous metrics have been proposed to quantify landscape composition, configuration and connectivity (Šímová and Gdulová 2012; Sklenicka et al. 2014), covering the patch size, dominance, shape complexity, fragmentation, connectivity, landscape diversity, contagion and aggregation (Mcgarigal and Marks 1995). We used these metrics to quantify the character of habitat and surrounding landscape matrices to investigate their effects on waterbird diversity.

Moreover, birds respond to their environment differently at different spatial scales and hence different conservation plans are needed across scales (Wiens 1989; Zhang et al. 2018). The surrounding environment tend to play a more important role at coarser scales as birds avoid areas highly disturbed by human activities

(Si et al. 2020), which often are a large component of landscape matrices (Herbert et al. 2018; Souza et al. 2019). However, the understanding of how landscape matrices affect bird diversity across spatial scales, in particular at coarse scales, is rather limited. Previous studies (Chan et al. 2007; Guadagnin and Maltchik 2007; De Camargo et al. 2018) investigating the effect of habitat and the surroundings on bird communities mainly focus on fine scales (500 m to 10 km). Considering that the maximum mean foraging flight distances of ducks and geese is 32. 5 km (Johnson et al. 2014) and is generally < 50 km (Ackerman et al. 2006; Si et al. 2011; Johnson et al. 2014), we chose the spatial scale > 10 km and < 50 km as the coarse scales to further investigate how the landscape features influence waterbird diversity.

This study investigates how habitat and landscape matrices affect waterbird diversity in the Yangtze River Floodplain across spatial scales using spatial and ordinary least squares regression models. We hypothesize that (1) habitat and landscape matrices jointly affect waterbird diversity, and (2) the effect of landscape matrices outweighs that of habitats at coarse scales.

Methods

Study area

The Yangtze River Floodplain (thereafter YRF, 28.3°–33.6° N, 112.2°–122.5° E; Fig. 1) is located in the humid subtropical climate zone. The annual average temperature ranges from 14 °C to 18 °C and average annual rainfall is from 1, 000 mm to 1, 400 mm (Xie et al. 2017; Wei et al. 2019). In this region, 11 Ramsar sites (wetlands of international importance, designated under the Ramsar Convention; http://www.ramsar.org) and 31 wetlands (including 10 national and 21 provincial-level wetlands) are designated as protected areas. A seasonal flood-drought cycle results in high water levels in spring and summer, followed by low water level in autumn and winter (Wei et al. 2019). Flooding brings nutrients and organic matter into the wetlands, during drought cycles as water levels decline, the large number of wetlands provide abundant feeding areas for waterbirds (Xu et al. 2017; Wei et al. 2019). YRF, as an important wintering area for local and migratory birds along the East Asian-Australasian Flyway, is composed of variable types of wetlands such as flooded wetlands, inland marshes, swamps and mudflats.

YRF is one of the Global 200 priority ecoregions for conservation identified by the World Wide Fund for Nature (Olson et al. 1998), and it provides habitat for about one million wintering waterbirds (Wang et al. 2017). Meanwhile, YRF, flowing through Shanghai and Hunan, Hubei, Jiangxi, Anhui and Jiangsu provinces, plays an important role in Chinese economy, agriculture and industry (Hollert 2013), support 29% of China's population (about 400 million) and produces more than 40% of the national GDP (Wang et al. 2017). Intensive human activities (such as agriculture, urbanization, land reclamation and conversion, etc.) in this region makes YRF one of the most critical and endangered ecoregions in the world (Olson and Dinerstein 2002). Thus, YRF is an appropriate region to explore how species diversity responds to the altered landscape patterns. There is an urgent need to generate sustainable development plans to solve the conflicts between economic development and biodiversity conservation in YRF.

Waterbird survey data

We obtained the waterbird survey data for 101 sites along YRF from The World Wide Fund for Nature (WWF; survey was carried out from 9 to 13 January 2011). This time of year was chosen because the distribution of wintering birds is relatively stable and concentrated. The survey sites where bird congregate were identified based on expert knowledge. Various methods were used to approach the survey sites. The survey team usually drove as close as possible and then walked on foot. Birds were counted by experienced field ornithologists from early morning and through the day using telescope, in at least two locations of one surveyed wetland. A total of 136 waterbird species were recorded during the survey. In some regions, only data at the county level was summarized and the counts corresponding to specific wetlands were not available. For example, the count in the Xingzi County (Jiangxi Province, China) is the sum of three wetlands. We excluded these records and only used data for sites with accurate geographical locations of a specific wetland and corresponding bird counts for further analyses (Fig. 1).

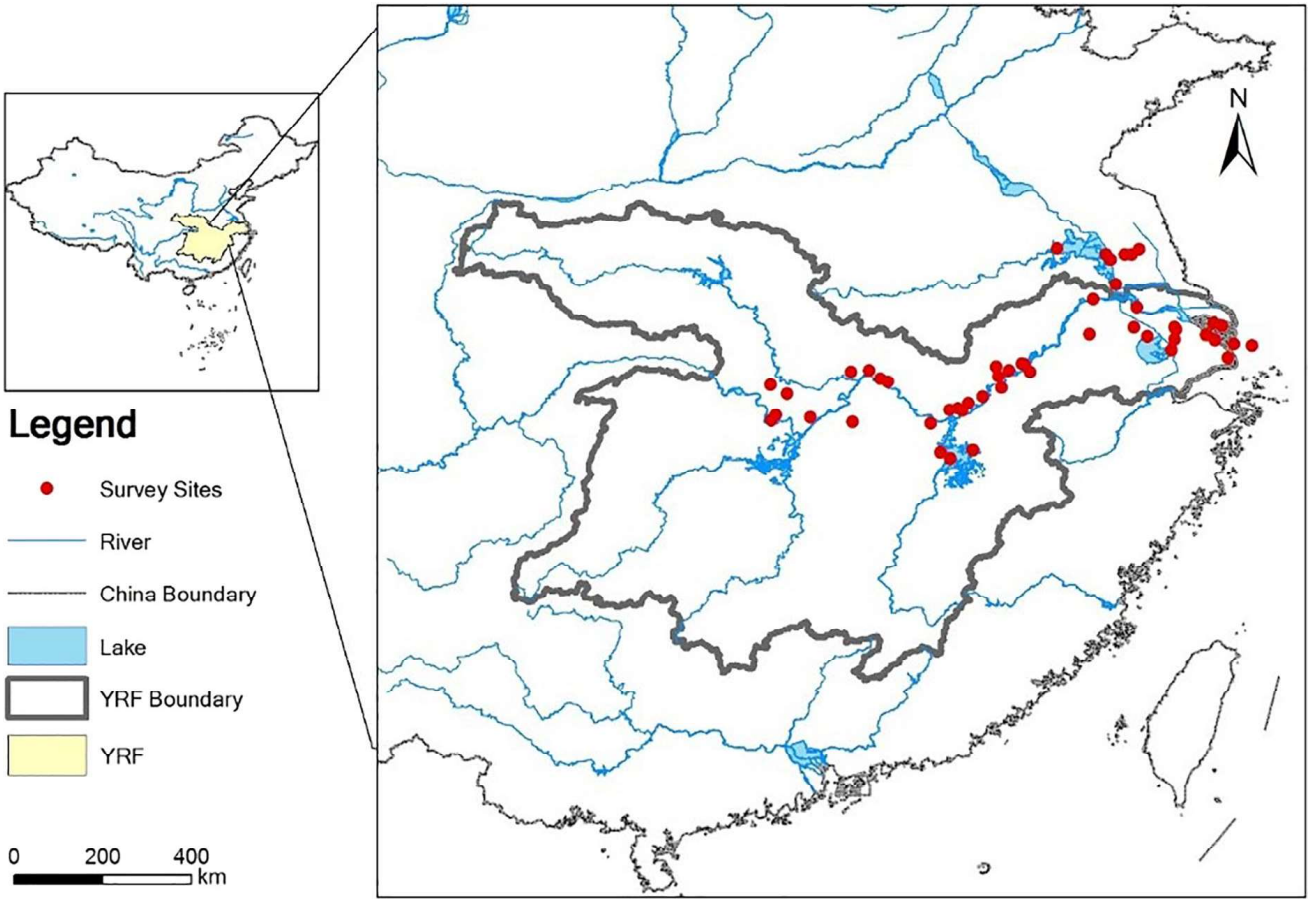

Fig. 1 Location of the Yangtze River Floodplain (YRF) and waterbird survey sites (red dots)

Land cover map

We used the aggregation land cover map of the finer resolution observation and monitoring of global land cover in 2010 (FROM-GLC-agg; http://data.ess.tsinghua.edu.cn; Yu et al. 2014) to calculate landscape metrics. According to the classification scheme of Li et al. (2016), we reclassified land cover map into nine types: cropland, forest, grassland, shrub, wetland, water, developed area and bareland. As wetlands are difficult to characterize by automatic classification (Yu et al. 2016), we replaced the water and wetland classifications in the FROM-GLC map with a 2008 wetland map generated based on human interpretation and multi-temporal imagery (Niu et al. 2012). Specifically, with the wetland map, 'water' is composed of recreational waters, artificial channels and fish farms, and 'wetland' includes shallow beaches, coastal marshes, estuary deltas, flooded wetlands and inland marshes. We then categorized land-use types into waterbird habitat (wetland, water, grassland, and shrub) and the surrounding landscape matrix (cropland, forest, bareland, and developed area). Grassland and shrub were included as habitat because grass is a potential food resource for some waterbirds and shrub could be used for resting or roosting. Cropland was classified as the landscape matrix due to a limited number of observed waterbird species in this land cover type (12/136 species).

Waterbird diversity

The Shannon-Wiener index has been frequently used to measure species diversity (Macarthur 1955; Lin et al. 2011; Dronova et al. 2016). It combine richness and evenness and can be used to compare the species diversity among different sites (Payne et al. 2005; Lin et al. 2011). The index (Hill 1973) is calculated for each site by Eq. (1):

$$H' = -\sum_{i}^{s} P_i lnP_i \quad (1)$$

where s is the total number of species and P_i is the proportion of individuals of species i to the total individuals of all species.

Landscape metrics at fine and coarse spatial scales

To quantify the habitat feature and landscape matrices, we generated circular buffers around the locations of sites at different spatial scales i.e., 5 km, 10 km, 20 km, 25 km, 40 km and 50 km, as the radii. We defined 5 km- and 10 km-scale as the fine scales (Forcey et al. 2011; Morelli et al. 2013), and scales larger than 10 km-scale as the coarse scales.

Landscape metrics were selected based on the life-history and ecological characteristics of waterbirds (Madsen 1985; Si et al. 2011; Li et al. 2017; Zhang et al. 2018). Table 1 lists the selected metrics covering multiple forms of patch size, dominance, shape complexity, fragmentation, connectivity, landscape diversity, contagion and aggregation (Mcgarigal and Marks 1995). For patch size and shape complexity, we also calculated their mean, minimum, maximum and standard deviation. Patch size includes patch area (PA) and patch core area (PCO), with a higher value indicating a larger patch. The core area represents the interior area of a patch after a user-specified edge buffer is eliminated. Smaller patches with greater shape complexity have a smaller PCO (Mcgarigal and Marks 1995; De Smith et al. 2007). Metrics for shape complexity include perimeter area ratio (PAR), shape index (SI) of each land cover type. Higher PAR and SI indicate greater shape complexity or greater deviation from regular geometry. Patch density (PD) and splitting index (SPI) (Green et al. 2017) represent the fragmentation level, while patch cohesion index (PCI) (Concepcion et al. 2016) indicates the connectivity level. Higher values of PD and SPI indicate more isolated patches, whereas higher PCI indicates more connected patches. Landscape Shannon index (LSHD) indicates the level of landscape diversity, with a higher value representing higher heterogeneity of patches in the landscape. Contagion index (CI) and aggregation index (AI; Li and Reynolds 1993) measure the extent of aggregation of patches for one particular land cover type. CI and AI increase if a landscape is dominated by large and well-connected patches. Landscape metrics were calculated in R 3.3.3 using the package 'SDMTools'. All metrics were standardized using z-score normalization transformation for the further analyses.

Statistical analyses

We first tested the influence of each landscape metric on waterbird diversity using univariate linear regression. Only significant metrics (p value < 0.05) were included (Forcey et al. 2011). A preselection was then carried out to exclude metrics with relatively high autocorrelation or high collinearity. Specifically, we used Moran's I to detect autocorrelation and metrics with a Moran's I larger than 0.5 or smaller than -0.5 were removed. We then use Variance Inflation Factors (VIF; Marquardt 1970) to diagnose collinearity. VIF measures the amount of multicollinearity in a set of multiple regression variables and tests the multiple correlation coefficient between one variable and the rest of variables. Specifically, we dropped the metric with relatively less impact (based on the result of the univariate linear regression), and repeated this process until VIFs of each variable were < 10. Considering the potential spatial dependency among survey sites, we used both spatial regressions (the spatial lag model SLM and the spatial error model SEM) and the Ordinary Partial Least Squares (OLS) regression. The non-significant metrics were removed, and variables kept in the final model were considered as key landscape metrics.

Two spatial autoregressive models were used to detect the level of spatial autocorrelation. A matrix of spatial weights W was calculated based on Euclidean distances between survey sites. The one is the spatial lag model (SLM) that adds a lag term of the dependent variable y into the OLS model. This model explains the spatial interaction between survey sites based on their proximity, as given by Eq. (2):

$$y = \beta X + \rho W y + \varepsilon \quad (2)$$

where β is the correlation coefficient of the independent variable X, W is a spatial weights matrix indicating distance relationship between pairs of survey sites. ρ is the coefficient of the spatially lagged variable Wy on the matrix of weight W applied to response values from spatial neighbors of each survey site, and ε is the random error.

Table 1 Summary of the landscape metrics used for investigating the effect of habitat and surrounding matrices on waterbird diversity

Category	Landscape metrics	Abbreviation	Description
Patch size	Patch area	PA	Mean/Min/Max/SD PA: the average/smallest/largest/ standard deviation of all patch areas of a particular land cover type. SD PA indicates the level of deviation from the mean patch area for one particular land cover type
	Patch core area	PCO	Mean/Min/Max/SD PCO: the average/smallest/largest/standard deviation patch core area of a particular land cover type. SD PA indicates the level of deviation from the mean patch core area for one particular land cover type
Shape complexity	Perimeter area ratio of each land cover type	PAR	PAR $= \frac{p_j}{a_j}$, where p_j is the perimeter of patch j and a_j is the area of patch j. Mean/Min/Max/SD PAR: the average/smallest/largest/ standard deviation perimeter area ratio for one particular land cover type. SD PAR indicates the level of deviation from the mean perimeter area ratio for one particular land cover type
	Landscape shape index of land cover type	LSI	LSI $= \frac{0.25E}{\sqrt{A}}$, where E is the total edges of patches of one land cover type and A is the total landscape area
	Shape index of each patch	SI	Mean/Min/Max/SD SI: the average/smallest/largest/standard deviation shape index for one particular land cover type. SD SI indicates the level of deviation from the mean value of the shape index for one particular land cover type
Fragmentation	Patch density of each land cover type	PD	PD $= \frac{N_i}{A}$, where N_i is the total number of patches for the particular land cover type and A is the total landscape area
	Splitting Index	SPI	SPI $= \frac{A^2}{\sum_{i=1}^{m}\sum_{j=1}^{n} a_{ij}{}^2}$, a$ij$ is area of patch ij, A is total landscape area. The degree of patch isolation for one particular land cover type
Connectivity	Patch cohesion index	PCI	PCI $= 1 - \left(\sum_{j=1}^{m} p_j / \sum_{j=1}^{m} p_j\sqrt{a_j}\right)\left(1 - \frac{1}{\sqrt{A}}\right)^{-1}$, where m is the number of patches of each land cover type, a_j is the area of patch, p_j is the perimeter of patch j and A is the total landscape area
Diversity	Landscape Shannon diversity index	LSHD	LSHD $= -\sum_i^n P_i lnP_i$, where n is the number of land cover types and Pi is the percentage of land cover i
Contagion	Contagion index	CI	CI $= \left[1 + \frac{\sum_{i=1}^{m}\sum_{k=1}^{m}\left[(P_i)\left(\frac{g_{ik}}{\sum_{i=1}^{m} g_{ik}}\right)\right]\left[ln(P_i)\left(\frac{g_{ik}}{\sum_{i=1}^{m} g_{ik}}\right)\right]}{2ln(m)}\right]$, where P_i is the percentage of patch type i, g_{ik} is the number of patch type i, and m is the number of land cover types in a buffer. High CI indicates large and well-connected patches
Aggregation	Aggregation index	AI	AI $= \frac{g_{ii}}{max \rightarrow g_{ii}}$, g_{ii} is the number of like adjacencies between pixels of patch i based on the single-count method. $max \rightarrow g_{ii}$ is the maximum number of like adjacencies between pixels of patch i based on the single-count method. The value of AI ranges from 0 to 1, and high AI means more aggregated patches

The other model is the spatial error model (SEM) that estimates the spatial autocorrelation existing in the regression residuals of the neighboring location (i.e. the spatial error) of the OLS model, as given by Eq. (3):

$$y = \beta X + \lambda W\epsilon + \mu \quad (3)$$

where λ is the spatial autoregressive coefficient for the spatial error variable $W\epsilon$ and μ is the random factor of disturbances.

We fitted in total seven models for the fine (two models) and the coarse (five models) scales. The performance of OLS and spatial auto-regression

models were compared using Akaike Information Criterion (AIC). AIC, as a model selection criterion, has a sound likelihood framework, based on Kullback-Leibler information loss between estimates of the model and actual values and allows the comparisons among models (Burnham and Anderson 2004). A lower AIC value means better fit of the model, thus the model with the lowest AIC value is deemed as the best model. Spatial regressions were carried out in GeoDa and the other analyses in R 3.3.3 software.

Results

Waterbird diversity of the survey sites in the Yangtze River Floodplain measured by the Shannon-Wiener index is shown in Table S1. The Shannon-Wiener index values varies between 0 and 2.6877 (mean = 1.32 ± 0.69 SD). The highest waterbird diversity was found in the Poyang Lake Nature Reserve in Jiangxi Province, followed by Chen Lake and Liangzi Lake in Hubei province, while relatively lower Shannon-Wiener values occurred in Ge Lake in Jiangsu province, the Aquafarm of Jieshou Town in Anhui province and West Yangcheng Lake in Jiangsu province (Table S1).

At both fine and coarse scales, the p-value of λ in SLM and that of ρ in SEM were higher than 0.05, which indicated that no strong spatial autocorrelation was observed among survey sites. Thus, we retained OLS models to estimate the influence of landscape features on waterbird diversity (Table 2).

According to the coefficient of each significant metric (Table 2; Fig. 2), we found waterbird diversity was strongly associated with the surrounding landscape matrix at both fine and coarse scales, and the effect was stronger at the coarse scales. At fine scales, a higher waterbird diversity was associated with a lower connectivity of developed area (i.e., lower PCI, a negative effect). At coarse scales, developed area showed the most pronounced effect on waterbird diversity, i.e., habitats surrounded by developed area of regular shapes (i.e., higher LSI, a positive effect) tended to have a higher waterbird diversity (Fig. 2). In addition, regular-shaped croplands (i.e. higher LSI, Mean SI and SD SI; positive effects) and larger irregular-shaped forest patches (i.e. higher Min SI and Mean PCA; positive effects) facilitated a higher waterbird diversity.

Significant relationships between habitat features and waterbird diversity were found at both fine and coarse scales (Table 2). At fine scales, the important variables included patch density (PD) of grassland and SD shape index (SD SI) of shrub. Waterbird diversity was significantly higher in more connected grassland (i.e. lower PD, a negative effect) and more irregular-shaped shrub (i.e. higher SD SI, a positive effect). At coarse scales, the important variables were the landscape shape index (LSI), the splitting index of shrub, the Mean shape index (Mean SI) and aggregation index (AI) of wetland. Irregular-shaped and well-connected wetland (i.e. higher Mean SI and AI, a positive effect), as well as irregular-shaped shrub (i.e. higher LSI, a positive effect) contributed to a high waterbird diversity whereas the isolated shrub (i.e. higher SI, a negative effect) resulted in a low waterbird diversity.

Discussion

This study investigated the impact of habitat features and landscape matrices on waterbird diversity across spatial scales. At fine scales, well-connected habitats (grassland and shrub) surrounded by isolated and regular-shaped developed area helped maintain high waterbird diversity. At coarse scales, waterbird diversity was higher in areas where aggregated wetlands were surrounded by regular-shaped developed area and croplands, and large irregular-shaped forests. Developed areas consistently influenced waterbird diversity and showed the most pronounced effect at coarse scales. The landscape matrix in which wildlife habitat is embedded should be managed wherever possible (Prugh et al. 2008; Franklin and Lindenmayer 2009), especially when expanding the developed area.

Waterbird diversity was negatively correlated with fragmentated habitats (i.e., isolated grassland, regular and isolated shrub and unconnected wetland with regular boundaries). Well-connected grassland, shrub and wetland habitat provide important foraging and resting area for waterbirds (Stafford et al. 2009; Pearse et al. 2012). Connectivity, at both fine and coarse scales, is important for waterbird aggregation (Guadagnin and Maltchik 2007). At finer scales, well-connected habitats facilitate the movement of waterbirds between feeding and roosting sites (Elphick

Table 2 The influence of landscape features on waterbird diversity in the Yangtze River Floodplain at fine and coarse scales

Scale	Buffer	Model	Dependent variable: Shannon–Winner index of waterbirds			
		Independent variable	Coefficient	P-value	Adjust R^2 (OLS)	AIC (OLS)
Fine scale	5 km	− the PCI of developed area	− 0.490	0.024*	0.283	82.081
		− the PD of grassland	− 0.350	0.001**		
	10 km	− the SD SI of developed area	− 1.126	0.042*	0.514	30.311
		+ the SD SI of shrub	3.179	0.003**		
Coarse scale	15 km	+ the LSI of shrub	0.053	0.013*	0.303	51.813
		− the LSI of cropland	− 0.004	0.008**		
	20 km	− the Mean SI of cropland	− 2.260	0.031*	0.233	77.635
		+ the Mean SI of wetland	1.442	0.005**		
	30 km	− the SD SI of cropland	− 0.810	0.029*	0.139	99.897
		+ the AI of wetland	0.106	0.031*		
	40 km	− the Mean SI of developed area	− 4.458	0.001**	0.235	97.674
		+ the Mean PCA of forest	1.567e-6	0.012*		
		+ the Min SI of forest	2.733	0.013*		
	50 km	− the Mean SI of developed area	− 2.887	0.015*	0.160	100.302
		− the SPI of shrub	− 1.123e-4	0.027*		

'+' means positive effects while '−' means negative effects

The credible interval of the estimate is 95%. *P < 0.05 (two-sided test), **P < 0.01 (two-sided test), ***P < 0.001 (two-sided test)
Landscape metrics: PCI patch cohesion index, PD patch density, SD SI standard deviation of shape index, LSI landscape shape index, Mean SI mean shape index, AI aggregation index, Mean PCA mean patch core area, Min SI minimum shape index, SPI splitting index

2008), which can reduce the costs due to shorter foraging flight distances. In addition, we found that waterbird diversity was lower in sites with regular-shaped shrub and wetland patches at coarser scales. In general, the regular and less complex patches are often associated with intensive human influnce (Mcgarigal and Marks 1995; Cunningham and Johnson 2011), whereas less disturbed patches are more complex (Krauss and Klein 2004). Furthermore, habitat patches with a higher shape complexity tended to have increased foraging resources (Andrade et al. 2018). Therefore, irregular-shaped shrub and wetland habitat helped to maintain a higher waterbird diversity due to the lower level of human disturbance and the higher level of potential food resources.

Developed area was the most critical factor influencing waterbird diversity, particularly at coarse scales. Though a previous study found that the presence of developed area negatively influenced waterbird richness (Rosa et al. 2003), we suggest that habitat surrounded by isolated or regular-shaped developed area can help to maintain higher waterbird diversity. Isolated developed area indicated a lower level of connectivity of surrounding patches, resulting in a higher connectivity of waterbird habitat patches (Pearce et al. 2007; Larsonab and Perrings 2013). In other words, well-connected surrounding landscape patches (i.e. developed area) indicated higher habitat degradation and fragmentation, which leads to a lower waterbird diversity. In particular, the effect of shape complexity of developed area was more prominent. Waterbird diversity decreased as the shape complexity of surrounding developed area increased. Surrounding developed patches with a more complex shape tended to have a longer border with the adjacent natural habitats, indicating a higher level of human disturbance (Gyenizse et al. 2014). Regular-shaped developed patches resulted in less disturbance to the habitat and hence support higher waterbird diversity.

Other landscape matrices, such as cropland and forest, also affected waterbird diversity. Regular-shaped cropland and larger irregular-shaped forest tended to facilitate a higher waterbird diversity. Similar to the developed area, regular-shaped cropland

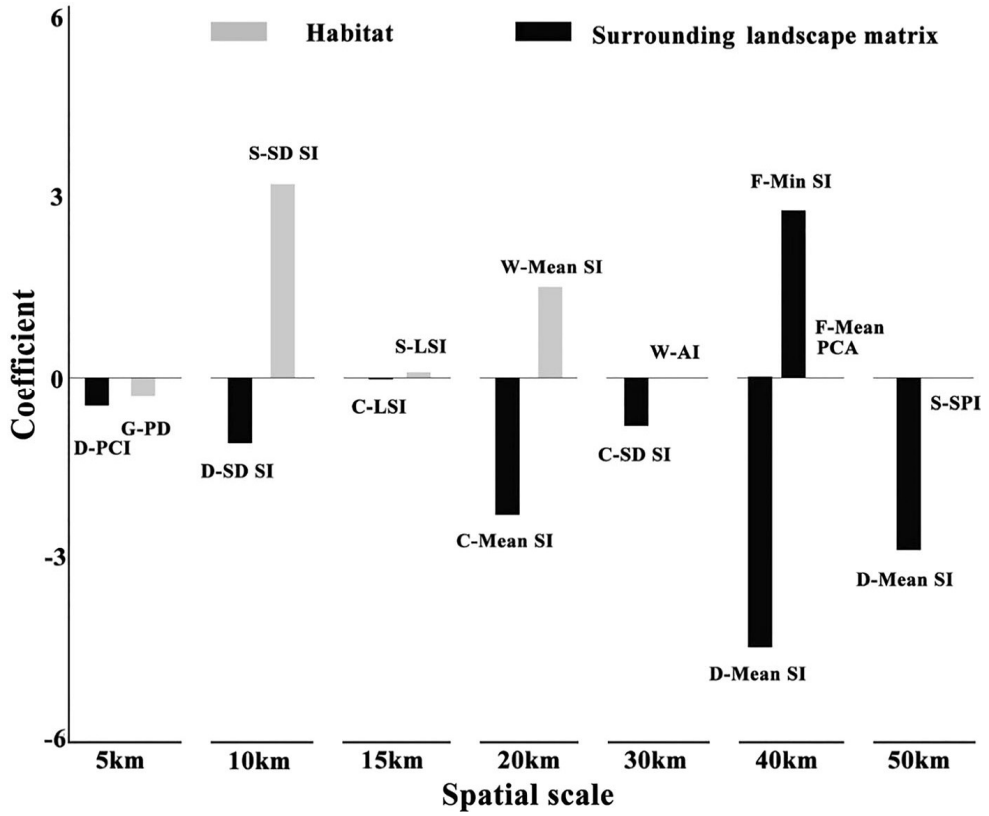

Fig. 2 Effects of landscape features on waterbird diversity along Yangtze River Floodplain. Black bars denote landscape matrices and grey bars denote habitat. The length of the bar depicts the coefficient of each metric representing the level of importance. Landscape metrics that have statistically significant values are displayed: D-PCI indicates the patch cohesion index (PCI) of developed area (D); G-PD means the patch density (PD) of grassland (G); D-SD SI indicates the standard deviation of shape index (SD SI) of developed area; S-SD SI means the SD SI of shrub (S); C-LSI indicates the landscape shape index (LSI) of cropland (C); S-LSI means the LSI of shrub; C-Mean SI indicates the mean shape index (Mean SI) of cropland; W-Mean SI means the Mean SI of wetland (W); C-SD SI indicates the SD SI of cropland; W-AI means the aggregation index (AI) of wetland; D-Mean SI indicates the Mean SI of developed area; F-Min SI means the minimum shape index (Min SI) of forest (F); F-Mean PCA means the mean patch core area (Mean PCA) of forest; D-Mean SI indicates the Mean SI of developed area; S-SPI means the splitting index (SPI) of shrub

indicated a lower level of habitat invasion and disturbance. Habitats surrounded by natural land tended to support more species due to relatively low human disturbance (Vandermeer and Carvajal 2001). Larger irregular-shaped forest patches could act as a buffer insulating core habitats from intensive human activities such as urban-rural development and agriculture expansion (Findlay and Houlahan 1997) thus facilitating a higher waterbird diversity.

We found that both habitat features and surrounding landscape matrices influenced waterbird diversity at fine scales, whereas at coarse scales the effect of the landscape matrix outweighed that of the habitat. At fine scales, waterbird diversity was facilitated by well-connected habitats surrounded by regular-shaped developed area. Whereas at coarse scales, the surrounding matrices (with the shape of developed area outperformed others) played the most important role in determining species diversity. The reason might be that initial habitat selection is mainly based on the appearance of the landscape (Moore and Aborn 2000), and birds tend to avoid regions with the habitat surrounded by well-connected landscape matrices. This kind of landscape tends to have more fragmented habitat patches and a relatively higher human disturbance. Among different types of landscape matrices, developed area had the most pronounced negative effect on waterbird diversity, probably because the level of human activity intensity is the highest in the developed area in comparison to other landscape matrices. We acknowledge that imperfect detection during surveys might negatively impact data quality

(false absences or false presence of species) and interpretation. We suggest increasing the number of surveys for each location in the future to further validate our findings.

Conclusion

Habitat features and landscape matrices jointly affected waterbird diversity, and the effect of the landscape matrix was more pronounced at coarse scales. Well-connected habitats (e.g. wetland, shrub and grassland) surrounded by isolated regular-shaped developed area and cropland, and large irregular-shaped forest helped maintain a higher waterbird diversity. Regular-shaped developed area was a critical factor that consistently facilitates a higher waterbird diversity across scales. Wetland managers should maintain well-connected habitats (wetland, grassland and shrub), and urban and rural landscape planners should minimize the expansion of developed areas to critical habitats and leave sufficient buffer to maintain the habitat connectivity and shape complexity in order to reduce the disturbance to birds. Our findings provide insights into understanding how waterbirds respond to altered landscapes and offer practical measures to help mitigate the human-bird conflicts in biodiversity hotspot areas.

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