The University Of Sheffield.

GLOBAL CHANGE AND THE FUTURE OF AVIAN DIVERSITY

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ABSTRACT

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Biodiversity in the Anthropocene is declining at an alarming rate. Both ecological and evolutionary components of biodiversity are critical for determining the processes that have led to the biogeographic patterns of biodiversity we see today, as well as understanding the impacts of global change on communities and ecosystems. Here, I use unique trait datasets, and phylogenetic relationships, to explore extant and future patterns of avian biodiversity.

In the first part of this Thesis, I interrogate global-scale biogeographic patterns of avian diversity, by using avian traits to reveal how species fill and expand niche space. I show that evolutionary history, rather than contemporary environment, drives patterns of extant global trait diversity. In the second part I assess the impact of species extinctions on this diversity and examine whether the loss of trait and phylogenetic diversity is greater than predicted by species loss alone. I find that not only is trait homogenisation expected across the whole Avian class, but that this is borne out spatially, with the majority of biome and ecoregion assemblages predicted to experience a significant reduction in morphological diversity with important consequences for ecosystem functioning. Finally, given that Anthropogenic land-use change is experienced most intensely in the tropics, I move from a broad to local spatial scales, and highlight that the protection of secondary forests should be seen as a priority for the conservation of tropical biodiversity. Overall, this Thesis helps to further our understanding of the origins of biodiversity, and in the face of global change, its conservation.

DECLARATION

I confirm that the work submitted in this Thesis is my own, that I am the primary author, and corresponding author for all publications arising from this work. I include the following acknowledgments, and explicitly indicate contributions for jointly authored publications. I confirm that appropriate credit has also been given within the Thesis where reference has been made to the work of others.

My supervisors, Dr Gavin Thomas and Professor David Edwards provided detailed structural and editorial input on all chapters. Between us, we conceived the ideas and designed the methodology for all data **Chapters (2, 3 and 4)**.

Chapter 2, *Global biogeographic patterns of avian morphological diversity*, is published in its presented form in **Ecology Letters** (2022). Dr Jen Bright, Elliot Capp, Dr Chris Cooney, Dr Gavin Thomas, Zoë Varley, and I, collected data from museum specimens and designed analytical protocols for producing the beak shape dataset. I analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

Chapter 4, *The effects of tropical secondary forest regeneration on avian phylogenetic diversity*, is published in its presented form in **Journal of Applied Ecology** (2020). Data from relevant studies was collected by Dr Philip Martin, Catherine Sayer, and I. I analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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Being outside birding and bird ringing has played an important part of my life, particularly during this PhD, and I thank my friends in the Sorby Breck Bird Ringing Group for their companionship, and interesting conversations. The expeditions to France, Mongolia and remote Scottish and Welsh islands have helped keep me sane throughout the PhD! A particular thanks to Steve for his encouragement and support in gaining my Trainer's permit.

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CONTENTS

LIST OF FIGURES

Figure 0.1: Resplendent Quetzal (*Pharomachrus mocinno*) Male. 26th March 2022. San Gerardo de Dota, Costa Rica.

CHAPTER 1

General Introduction

1.1 Biodiversity and global change

What drives global variation in biodiversity and why are some regions so much more diverse than others (Currie et al., 1999; Gaston, 2000; MacArthur, 1965; Rohde, 1992)? The vast diversity of life on Earth, and its distribution, has fascinated biologists for centuries (Darwin, 1896, 1859; Humboldt, 1849; Wallace, 1871). For instance, why does a strong latitudinal increase in biodiversity towards the tropics exist, and why are tropical communities so species rich (Hillebrand, 2004; Lewinsohn and Roslin, 2008; Mittelbach et al., 2007; Rahbek, 1995)? Exploring and understanding questions such as these are central in determining the origin of biodiversity, and in the face of global change, its conservation. Indeed, we are currently living in the Anthropocene, a geological epoch defined by significant human impact on the planet, such as accelerated climatic change, and land surface change (Crutzen, 2002; Lewis and Maslin, 2015). Earth is now experiencing its sixth mass extinction event, with biodiversity in the Anthropocene declining at an alarming rate (Barnosky et al., 2011; Ceballos et al., 2015; Dirzo et al., 2014). Recent predictions suggest that in the last 100 years, 200 species of vertebrates have gone extinct, and that the current rate of extinction is up to 100 times higher than background levels (Barnosky et al., 2011; Ceballos et al., 2015).

The biggest anthropogenic driver of the biodiversity crisis is the conversion of pristine habitat for human use (e.g., deforestation, agricultural expansion etc.) (Laurance et al., 2014). To feed a growing population, land-use change is still accelerating, with the total land used globally for crops increasing by 9% from 2003 to 2019 (Potapov et al., 2021). The rate of land-use

change is particularly acute in the world's most species rich biomes, tropical rainforests (Laurance et al., 2014). Indeed, tropical rainforests were the primary source of new agricultural land in the 1980s and 1990s, with over 150 million hectares of forest converted to farmland between 1980 and 2012 (Gibbs et al., 2010; Hansen et al., 2013). Agricultural expansion and intensification have already led to widespread habitat loss and fragmentation, driving species extinctions, decreases in community diversity, and loss of ecosystem services (Devictor et al., 2008; Newbold et al., 2018; Potapov et al., 2021).

A further feature of the Anthropogenic biodiversity crisis is the increased incidence of biotic homogenisation (Clavel et al., 2011; McKinney and Lockwood, 1999; Socolar et al., 2016). Homogenisation occurs where a native set of diverse, often specialist endemic species, are replaced by a smaller number of more generalist, widespread species that are sometimes introduced by humans (McKinney and Lockwood, 1999; Olden et al., 2004; Blackburn et al., 2009, 2019) and thrive in human-altered environments (Thomas, 2013). The decline of Anthropocene "losers" is non-random, with, for example, species with small ranges (Newbold et al., 2018; Purvis et al., 2000), large body sizes (in birds, mammals, and cartilaginous fishes (Ripple et al., 2017), and specialists with narrow niche breadths (Clavel et al., 2011) being at particular risk of extinction. Biotic homogenisation is happening at a global scale, but we do not currently have a good idea of its impact across entire taxonomic groups or which regions of the world are most at risk. This is particularly important as biological homogenisation will lead to a considerable loss of ecological roles and ecosystem functions, including those currently important to humans as ecosystem services, and those whose benefits are yet to be realised (Clavel et al., 2011; Dirzo et al., 2014; Faith, 1992; Hooper et al., 2005).

With limited resources, it can be challenging to identify how best to focus conservation efforts to maximise global biodiversity protection (Vane-Wright et al., 1991; Wilson et al., 2006). Ordinarily, biodiversity loss is measured in terms of the number of species declining in a given area. However, species richness-based metrics of diversity consider all species as equally distinct units without considering variation in the evolutionary history, morphology, or ecological roles that each species represents (Devictor et al., 2010; Faith, 1992; Purvis and Hector, 2000). To capture these differences, two alternative measures of biodiversity are increasingly used: trait diversity and phylogenetic diversity (Faith, 1992; Petchey and Gaston, 2002; Tilman, 2001; Webb et al., 2002). Trait-based diversity metrics aim to capture organismal traits that enable species to occupy a particular ecological niche or ecosystem (Petchey and Gaston, 2002; Tilman, 2001). Phylogenetic diversity quantifies the total amount of evolutionary features that a community represents (Faith, 1992; Webb et al., 2002).

Both ecological and evolutionary components of biodiversity are critical for determining the processes that have led to the biogeographic patterns of biodiversity we see today, as well as understanding the impacts of global change on communities and ecosystems, and I identify the following key questions relating to trait and phylogenetic diversity.

i) How is phylogenetic diversity distributed globally?

ii) How is trait diversity distributed globally?

iii) Do species extinctions lead to homogenisation of trait and phylogenetic diversity?

iv) Can phylogenetic diversity recover after land-use change?

In the next section I expand on these questions before introducing the history, uses and conservation of trait diversity and phylogenetic diversity, before discussing why phylogenetic diversity can not necessarily be expected to capture trait diversity.

1.2 Key questions

How is phylogenetic diversity distributed globally?

Understanding the phylogenetic structure of assemblages can reveal the origins and drivers of biogeographic patterns across the globe for many taxonomic groups (e.g., Cavender-Bares et al., 2009; Davies and Buckley, 2011; Fritz and Rahbek, 2012; Safi et al., 2011; Vamosi et al., 2009; Voskamp et al., 2017; Webb et al., 2002). Phylogenetic diversity is expected to correlate with species richness because the addition of species to a community also adds a branch length to the community phylogenetic tree. However, deviations from this *a priori* relationship are widely observed (Davies and Buckley, 2011; Forest et al., 2007; Fritz and Rahbek, 2012; Voskamp et al., 2017) and can reveal phylogenetic overdispersion or clustering in communities, where species are less or more related than expected (given species richness) respectively (Vamosi et al., 2009; Webb et al., 2002). For example, the Western Amazon has recently been highlighted as an evolutionary "cradle" of freshwater fish biodiversity, with communities showing strong phylogenetic clustering, suggesting that they are comprised largely of recent radiations (Salgueiro et al., 2022). Phylogenetic clustering has also been observed at higher latitudes across many taxa including soil microbes (Bryant et al., 2008), hummingbirds (Graham et al., 2009), temperate angiosperms (Qian et al., 2014), butterflies (Pellissier et al., 2013), geometrid moths (Brehm et al., 2013), and frugivorous birds (Dehling et al., 2014). Abiotic conditions tend to be more extreme at higher elevations, and so environmental filtering is likely to both reduce the number of species that can exist in such conditions, and result in more closely related species with similar traits (Dehling et al., 2014).

At a global scale, phylogenetic diversity is distributed unevenly, and as expected, broadly maps to species richness (Voskamp et al., 2017). Areas of high altitude, such as the Andes and

Himalayas have lower than expected avian phylogenetic diversity, as do areas in the Northern Hemisphere that were covered during the last glacial maximum, whereas isolated oceanic islands have greater phylogenetic diversity than expected (Voskamp et al., 2017). In 2016, at the start of my PhD, I undertook some initial work to map where extant avian phylogenetic diversity was greater or lower than expected across and within each biogeographic realm (Holt et al., 2013) (**Figure 1.1**). To do this, I calculated the predicted phylogenetic diversity of null communities generated from biogeographic realm species pools and compared values to the actual phylogenetic diversity of communities (i.e., standard effect sizes), whereas Voskamp et al. (2017) used regression residuals from the relationship between species richness and phylogenetic diversity. One finding, was that within the Neotropical realm, the Amazon rainforest and surrounding lowlands have higher than expected phylogenetic diversity compared to the Andes. The Andes contain coexisting close relatives from families such as hummingbirds (Trochilidae) (Graham et al., 2009), and high turnover (β-diversity) of communities along extreme altitudinal gradients (Jarzyna et al., 2021; Voskamp et al., 2017). Over recent years, exploring global distributions of phylogenetic diversity has advanced our knowledge of the origins and maintenance of biogeographic patterns (Safi et al., 2011; Voskamp et al., 2017). However, compared to phylogenetic diversity, there is a relative paucity of studies investigating the global distributions of trait diversity.

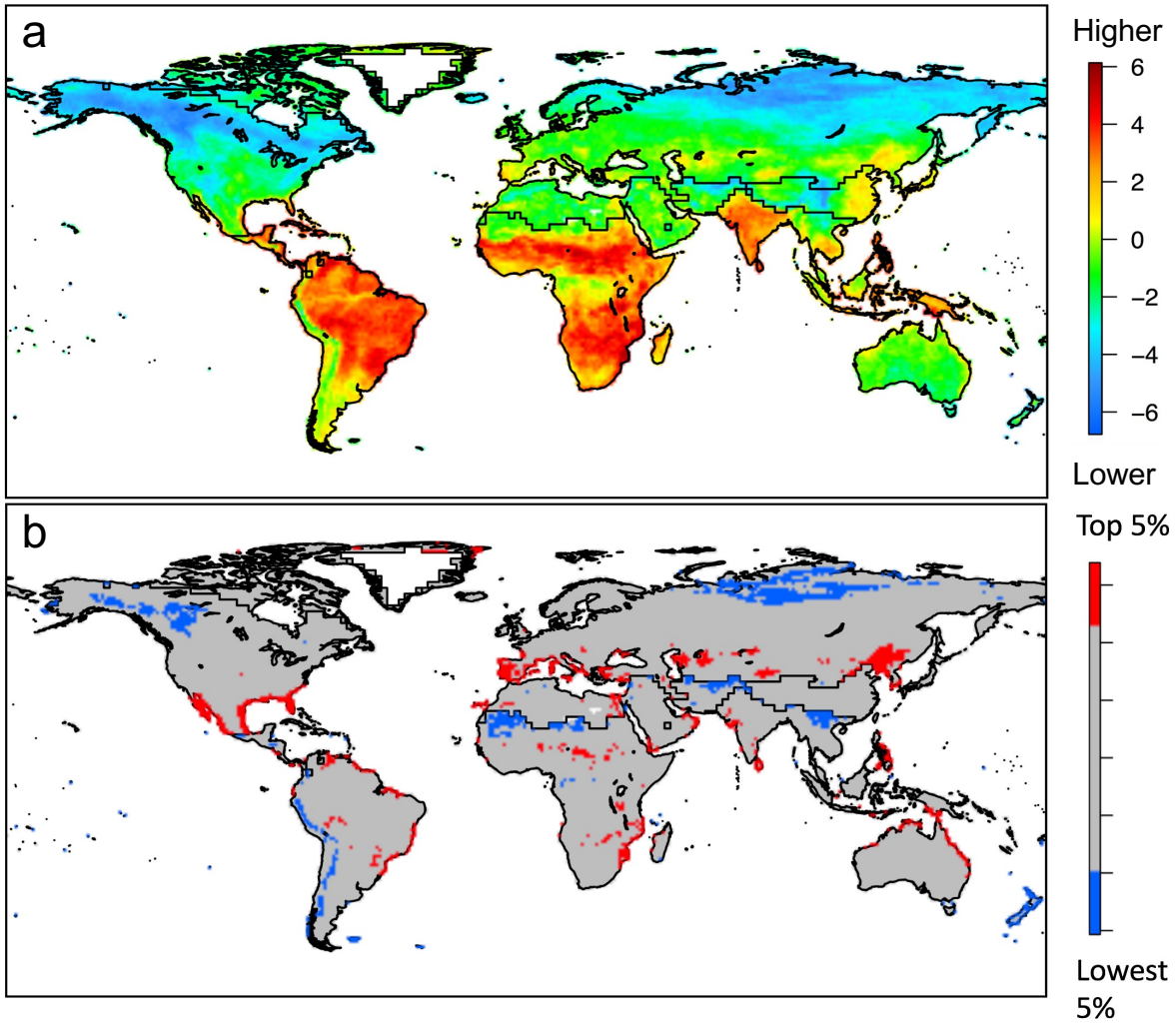

Figure 1.1: Global maps showing **a)** areas across all realms with higher and lower than expected phylogenetic diversity (sesPD) in warmer and cooler colours respectively, and **b)** grid cells containing the highest (red) or lowest (blue) 5% of sesPD values within each realm, with the remaining cells masked in grey. Breeding range maps for 9750 species were downloaded from BirdLife International (http://www.birdlife.org/datazone/home) and used to generate a global terrestrial presence/ absence matrix at a 100km x 100km grid cell resolution. SesPD was calculated from random draws from species pools restricted to each biogeographic realm (Holt et al., 2007).

How is trait diversity distributed globally?

Over recent years, the increasing availability of novel, high-quality trait data, for a wide range of taxa, has accelerated the use of trait diversity metrics in understanding how communities are structured (e.g., Pigot et al., 2016), how morphological form maps to ecological roles and/

or functions (Anderson et al., 2011; Bright et al., 2019, 2016; Miller et al., 2017; Navalón et al., 2019; Olsen, 2017; Pigot et al., 2020), and how trait diversity has accumulated over evolutionary time (Chira et al., 2018; Cooney et al., 2017). However, with a few exceptions (e.g., (McLean et al., 2021; Sheard et al., 2020)), we lack a good understanding of the biogeographical patterns of trait diversity across the globe. Unravelling this could provide important insight into community structure at a global scale.

Species can fill niches in at least two different ways, through niche "expansion" where increasing species richness leads to niche space increases, and through niche "packing" where niche space becomes more densely occupied as species are added (MacArthur, 1965). Trait diversity metrics can reveal regions of exceptional spread and density of species traits, allowing longstanding hypotheses into global patterns of biodiversity, such as MacArthur's (1965) niche "packing" and "expansion" models, to be investigated. Furthermore, investigating the way communities fill trait space can reveal how patterns of species richness have arisen, such as how the tropics can harbour such high levels of species.

As well as mapping the biogeographical distribution of extant trait diversity, unravelling the environmental, and evolutionary factors that have shaped this diversity is essential if we are to determine its origins, and ultimately its conservation. Such drivers have been investigated at a variety of spatial scales. For example, historical megafaunal mammal herbivory and soil fertility were significant drivers of the patterns of plant trait diversity we see today in the Neotropics (Dantas and Pausas, 2022). A key knowledge gap is investigating the macroecological and evolutionary factors that have driven trait diversity both within and between assemblages across the globe.

Do species extinctions lead to homogenisation of trait and phylogenetic diversity?

In the face of increasing Anthropogenic induced global change, understanding the impacts on trait and phylogenetic diversity has never been more important given the potential reduction of ecological traits, evolutionary features, and ecosystem functioning (Devictor et al., 2010; Faith, 1992; Purvis and Hector, 2000). Both measures are sensitive to the non-random loss of species (Cardillo et al., 2005) and can reveal where species extinctions are expected to lead to biotic homogenisation (Clavel et al., 2011; Daru et al., 2021; McKinney and Lockwood, 1999). This is because extinction risk is not distributed equally across the tree of life or between functional groups of species (Cardillo et al., 2008; Dirzo et al., 2014; Lee and Jetz, 2011; Ripple et al., 2017). Whilst some research has assessed the projected loss of phylogenetic and trait diversity for a variety of taxa (e.g., (Brodie et al., 2021; Cooke et al., 2019; Oliveira et al., 2020), the picture is far from complete. As well as being non-random across the phylogeny and between functional groups, extinction risk is also spatially variable. This is because the threats faced by species (e.g., hunting, habitat loss, climate change), and their sensitivities to such threats vary across space (Brodie et al., 2021; Davies, 2019; Harfoot et al., 2021). As a result, endangered and threatened species occur in higher frequencies in certain regions. These areas are therefore at increased risk of trait and phylogenetic homogenisation. Identifying the areas likely to be at immediate risk is an important outstanding goal, given the increasing threat and intensity of anthropogenic induced change on biodiversity.

Can phylogenetic diversity recover after land-use change?

Phylogenetic diversity is increasingly considered an important metric for assessing contemporary anthropogenic impacts. The conversion of tropical forests to agriculture is one

of the biggest drivers of global species richness loss, and recent studies have investigated its impact on local phylogenetic diversity. For example, along a gradient of agricultural land-use types in Costa Rica, phylogenetic diversity was found to be 15% and 40% lower in diversified agriculture and intensive monocultures respectively compared to avian forest communities (Frishkoff et al., 2014), and this loss was driven by increases in species relatedness and a decline in species richness (Edwards et al., 2017; Frishkoff et al., 2014). However, in many areas, agricultural land has been abandoned resulting in increases of secondary forest regrowth (Aide et al., 2013; Hurtt et al., 2017). Species richness often recovers as secondary forests age (Acevedo-Charry and Aide, 2019; Barlow et al., 2007; Gilroy et al., 2014), however, our knowledge of how biodiversity metrics other than species richness differs between primary and secondary forests is limited. Recent work has found that in the Neotropics, the regeneration of secondary tropical forests on abandoned farmland can lead to recovery of phylogenetic diversity (Edwards et al., 2017, Edwards et al., 2021). Whether this finding is applicable across the tropics is currently unknown.

A further impact to biodiversity following the conversion of primary forest to agriculture is the loss of forest-dependent, disturbance sensitive species, and the gain of more disturbance tolerant, open habitat specialists. Phylogenetic diversity declines rapidly with increasing agricultural intensification (Frishkoff et al., 2014; Prescott et al., 2016). In addition, whilst species richness may recover quickly following agricultural abandonment, the resultant community may differ substantially in terms of its structure and phylogenetic composition. Secondary forest communities could therefore contain species that are much more closely related than those in primary forest communities, with more evolutionarily distinct species lost. Unravelling whether secondary forests represent an important reservoir of phylogenetic

diversity, and comparable community composition to primary forests is a key priority given that secondary forests are at near constant threat of reconversion to farmland, and even targeted to prevent them being reclassified as forest (Reid et al., 2018; Sierra and Russman, 2006).

1.3 Trait diversity

Historical overview

For many centuries, biologists have pondered on the huge diversity of species forms, and how this diversity may have consequences for the functioning of ecosystems (Laureto et al., 2015). For example, Darwin noted that areas of higher plant diversity were linked to higher productivity (Darwin, 1859). Indeed, measuring the diversity of traits that taxa in a community possess can be a stronger predictor of ecosystem functioning than species richness (Hooper et al., 2005; Tilman et al., 1997), although this relationship is mixed and often dependent on the specific metrics used to capture trait diversity (Flynn et al., 2011; Mouillot et al., 2011).

An ecosystem containing a community of species with diverse traits has more functions than an ecosystem of species with lower trait diversity. As such, species have traditionally been grouped according to their "functional" traits that influence one or more aspects of ecosystem functioning (Cadotte et al., 2009; Tilman, 2001; Tilman et al., 1997). Despite its logic, methods of grouping species that do not suffer from being arbitrary, and that allow significant differences between species groups to be identified are not straightforward (Diaz and Cabido, 2001; Petchey and Gaston, 2002; Tilman, 2001). A plethora of measures for quantifying trait diversity have been proposed (Laureto et al., 2015; Pavoine and Bonsall, 2011; Petchey and Gaston, 2002), as well as different methods for selecting and defining sets

of species traits (e.g., morphological traits, functional traits etc.) (Kohli and Jarynza, 2021; Guillerme et al., 2020a).

Species traits

The first step in quantifying any trait diversity metric is deciding which sets of traits to measure. This ultimately depends on the types of questions being asked, as well as the availability and quality of trait data. Classifying species into functional groups based on the scoring of functional roles (e.g., life history, behaviour, diet) is a pragmatic option where high-quality trait data are lacking but requires subjective decision making (Jones et al., 2009; Kohli and Jarzyna, 2021; McLean et al., 2021; Oliveira et al., 2017; Pigot et al., 2020, 2016; Wilman et al., 2014). For example, decisions are initially made on which categories are relevant (e.g., diet) and then again on how species are allocated to those categories ("Plant/seed", "Fruit/nectar", "Omnivore", "Invertebrate" etc.) (Wilman et al., 2014).

An alternative is to use ecologically relevant, continuous morphological traits that capture variation among and between functional groups (Kohli and Jarzyna, 2021; Pigot et al., 2020). Whilst still requiring decisions to be made about which traits to measure, this approach provides finer-grained resolution that distinguishes multiple morphologies filling a single functional role that could otherwise be lost when assigning species to functional categories (Pavoine and Bonsall, 2011). Furthermore, behavioural observations that enable dietary or foraging classification are often lacking for rare and cryptic species, and across large geographical scales. Recent research using simulations have shown that using coarser-grained data can lead to misleading conclusions regarding community structure, for example resulting in overestimates of the strength of trait convergence and underestimates of the prevalence

of ecological roles such as biotic interactions (Kohli and Jarzyna, 2021). Therefore, the use of quantitative, fine-resolution trait data is recommended where possible (Kohli and Jarzyna, 2021). The recent advent of novel, high-quality, comprehensive datasets for entire taxonomic groups (Jones et al., 2009; Oliveira et al., 2017; Tobias et al., 2022; Wilman et al., 2014) provides opportunity to quantitatively measure trait diversity in detail, across space and time.

Calculating trait diversity

There are many ways to quantify trait diversity, and some of the most well-used are those that quantify the diversity, or dissimilarity of species traits in an assemblage or community, using trait dendrograms and multidimensional spaces (Swenson, 2014). In the early 2000s, Petchey and Gaston (2002) proposed the use of dendrogram-based measures of trait-diversity. To create the dendrogram, a hierarchical clustering algorithm is used on an inputted Euclidean trait matrix. This allows distances between species to be measured in terms of branch lengths, and total trait diversity calculated by simply summing the branch lengths connecting species (Petchey and Gaston, 2002) in an approach analogous to measuring phylogenetic diversity (**Section 1.4**). One drawback to this approach is that this can remove fine-scale differences between traits (Swenson, 2014). More recently, methods to capture trait diversity have often been based on measuring Euclidean distances directly from multidimensional spaces (Guillerme et al., 2020a).

When plotting traits across multidimensional space, each dimension represents a different trait, and species are plotted according to the values of traits they possess. There are three main ways to broadly group existing metrics that quantify how species inhabit trait space: size, density, and position (**Figure 1.2**) (Guillerme et al., 2020b). Measuring the size, or volume

of trait space captures the overall spread of trait values in a community (**Figure 1.2a**). A community with greater values contains a greater diversity of traits, with organisms having more extreme trait values. Trait space size can be measured in several ways (e.g., hypervolume (Blonder, 2018), the sum of ranges, or the sum of variances (Foote, 1992; Wills, 2001)). Density measures (e.g., average pairwise distance (Foote, 1992; Harmon et al., 2008)), quantify how close together species are in trait space (**Figure 1.2b**), with lower values showing species are clustered in trait space, having more similar traits. These are less commonly used than size measures but give additional, ecologically relevant insight into community structure. For example, increasing density of species in trait space indicates niche "packing" with species filling similar ecological roles (MacArthur, 1965; Pigot et al., 2016). Finally, position metrics, whilst uncommonly measured, can show whether different communities contain different combinations of traits (**Figure 1.2c**) (Guillerme et al., 2020a; Mammola et al., 2019). With so many metrics, careful consideration of which to use is required, particularly as some metrics can capture multiple features of trait space (e.g., size and density), and this is often lacking in practice.

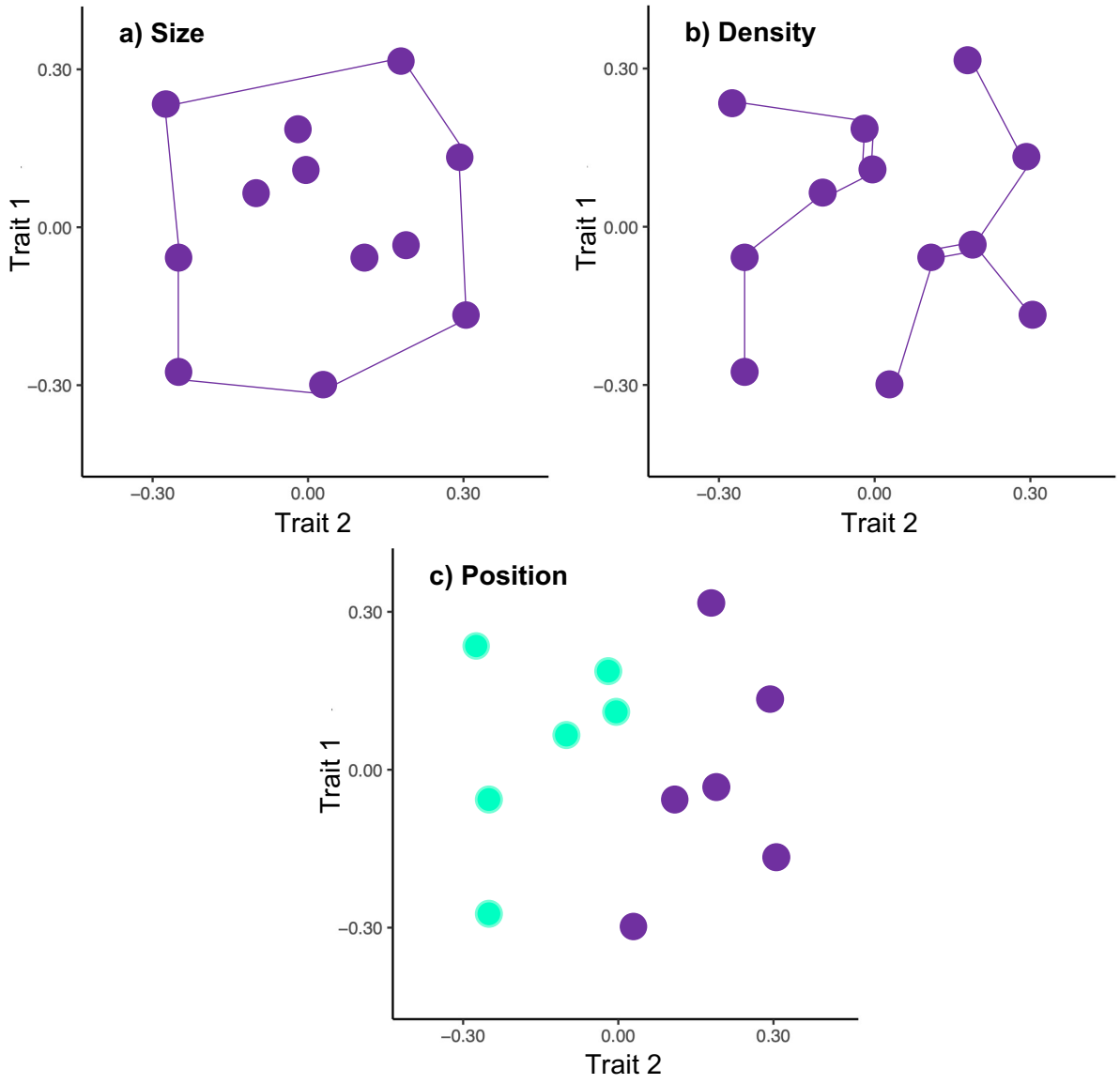

Figure 1.2: Illustration of the main three families of trait metrics in 2 dimensions. Each dot represents a species, and these are plotted for two trait values (Trait 1 and 2). a) the size that species occupy in morphospace is calculated as the volume of space filled. Here this would be the area with the solid lines. b) the density of species in morphospace gives a measure of how close together species are. Here the lines represent the nearest neighbour distance for each species. c) the position of one group (turquoise) relative to another (purple). Whilst occupying similar volumes of trait space, the trait combinations are clearly different.

1.4 Phylogenetic diversity

Historical overview

Phylogenetic diversity measures the total amount of evolutionary history or "features" represented by all species in that species set (Faith, 1992). In its simplest form, Faith's phylogenetic diversity is calculated by adding together all phylogenetic branch lengths connecting a group of taxa (**Figure 1.3**):

$$pd = \sum_{i}^{n} l^{i}$$

Where l^{i} is the branch length of taxon i, and there are n taxa present in the group.

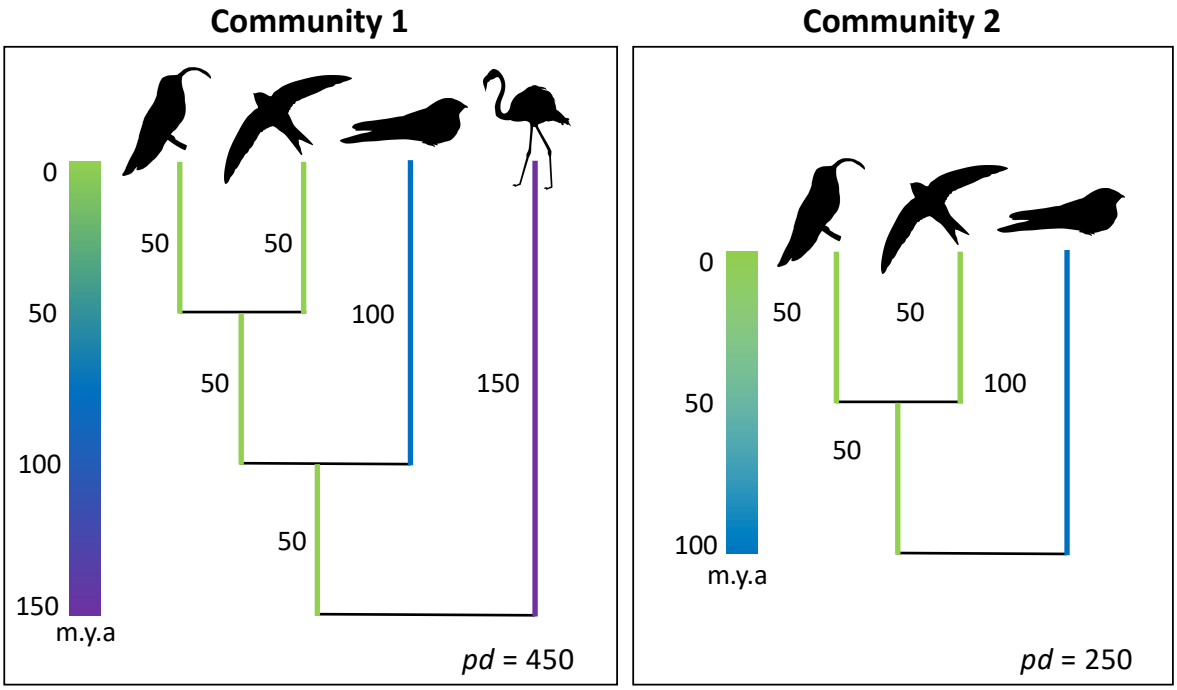

Figure 1.3: Illustration of how Faith's phylogenetic diversity is calculated and varies between different groups of taxa – in this case, two hypothetical bird communities. In community 1, a community of four species is connected by phylogenetic branches as shown. Faith's phylogenetic diversity is simply the sum of each branch length (in million years) connecting all species. For community 1 this is 450 million years, and for community 2, this is 250 million years. All bird silhouettes are in the public domain and were downloaded from Phylopic.org.

Phylogenetic diversity was originally introduced as a tool to aid conservation decision making with the aim of prioritising protection of taxa that represent the maximum underlying number of unique features (Faith, 1992; Vane-Wright et al., 1991). The longer the branch length, the more features are captured (Faith, 1992). As species and their traits diverge over time, more distantly related species will have more distinct traits (Redding and Mooers, 2006; Wiens and Graham, 2005). Phylogenetic diversity is a surrogate measure that has been argued to capture net divergence in all species traits, both measurable and unmeasurable, realised and yet to be realised. This characteristic means that conserving phylogenetic diversity can help to protect biodiversity option-value – whereby currently unrealised benefits of biodiversity are protected for future generations (Faith, 1992). More recently, phylogenetic diversity has been applied to community ecology (Webb et al., 2002) where it, for example, allows the identification of communities with higher vs lower phylogenetic diversity than expected (e.g., **Figure 1.3**).

1.5 Phylogeny as a proxy for trait diversity

Trait and phylogenetic diversity are amassed over long evolutionary time scales and are frequently considered to positively correlate such that communities with higher phylogenetic diversity contain species with a higher diversity of traits (Wiens and Graham, 2005). This can occur if species traits evolve at a constant rate (e.g., following Brownian motion (Felsenstein, 1985)). However, species traits do not always accumulate across the phylogeny at a constant rate (e.g., (Chira et al., 2018; Harmon et al., 2010; O'Meara et al., 2006; Venditti et al., 2011)). Consequently, the relationship between phylogenetic and trait diversity can deviate and the use of phylogenetic diversity as a proxy for trait diversity is hotly debated (Kelly et al., 2014; Mazel et al., 2018, 2017; Pavoine et al., 2013; Redding et al., 2010). However, phylogenetic

diversity quantifies the *total* feature diversity of species (Faith, 1992), and given that it is impossible to measure all species traits that enable a species to exist in its niche, it perhaps should not necessarily be an *a priori* expectation that phylogenetic diversity will strongly correlate with selected subsets of species traits (Tucker et al., 2018).

1.6 The conservation of trait and phylogenetic diversity

Trait diversity

Conserving trait diversity is likely to buffer against the decline of ecosystem functioning, and the loss of key ecosystem services (Dirzo et al., 2014; Hooper et al., 2005). Conservation mitigation schemes designed to conserve species richness do not always conserve equivalent trait diversity (Devictor et al., 2010). Some studies have also predicted that under particular scenarios, such as agricultural intensification, we could lose trait diversity at a greater rate than we lose numbers of species (Flynn et al., 2009; Sayer et al., 2017). Consequently, a multi-faceted approach to conservation seems crucial. Despite multiple calls for trait diversity to be considered when devising conservation programs, there has been very limited uptake in the use of these metrics (Devictor et al., 2010; Veron et al., 2017). In some respects, this may be because high-resolution range maps and detailed trait data are still not available, or only recently available, for many taxa or geographical regions. Furthermore, the ecological relevance of selected species traits is not always clear. Finally, a huge number of different diversity indices exist for calculating trait diversity, and so it may not be straightforward for conservation practitioners to identify which traits and metrics are best to use. Research therefore must focus on communicating the use of traits based on their ecological relevance and choosing trait diversity metrics that clearly complement the study aims.

Phylogenetic diversity

The conservation of phylogenetic diversity is important for several reasons. Firstly, as outlined previously, phylogenetic diversity can effectively capture the different evolutionary features of diversity (Faith, 1992; Owen et al., 2019), and can protect biodiversity option-value ensuring unrealised benefits of biodiversity are there in the future (Faith, 1992). Furthermore, there is intrinsic value in conserving as much of the world's evolutionary heritage as possible (Winter et al., 2013). Secondly, communities with high phylogenetic diversity are likely to hold relict or evolutionarily distinct species, with few close relatives (Jetz et al., 2014). The threat of extinction is not phylogenetically random (Bennett and Owens, 2002; Purvis et al., 2000; Vamosi and Wilson, 2008), and so phylogenetic diversity could be lost at a disproportionately greater rate than that predicted by random species extinctions alone (Oliveira et al., 2020). At a global scale, research has focused on whether conserving existing biodiversity hotspots and protected areas will adequately protect phylogenetic diversity as well (Daru et al., 2019; Devictor et al., 2010; Safi et al., 2013). More locally, strategies for conserving phylogenetic diversity have been identified, such as the use of land-sparing agriculture (where natural land is designated to be offset) being a better strategy than land-sharing ("wildlife-friendly" features are integrated within intensive agriculture) in the tropics (Edwards et al., 2021).

Nonetheless, since its inception in the early 1990s as a tool to prioritise conservation decision making in the face of limited resources (Faith, 1992; Vane-Wright et al., 1991), and considerable research highlighting its importance, the adoption of phylogenetic diversity by global conservation bodies and policyholders as a key biodiversity metric to conserve has been surprisingly low. In some respects, this may be because well resolved phylogenies and distributional data are still not available or have only become recently available for many taxa.

A major shift forwards was the development of the EDGE of existence program, launched by the Zoological Society of London (ZSL) in 2007 (Isaac et al., 2007; Redding and Mooers, 2006). It combines species relative contribution to phylogenetic diversity – Evolutionary Distinctiveness (ED) (Redding and Mooers, 2006) - with their threat status to identify species that are both Evolutionarily Distinct and Globally Endangered (EDGE) (Isaac et al., 2007) and is used to target practical conservation efforts to species, and EDGE zones – areas with a particularly high occurrence of EDGE species. The use of EDGE information has recently been included by the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES) as an indicator of biodiversity option-value (Davies et al., 2018).

1.7 Birds as a model system

Birds (class Aves) represent an ideal group of organisms to address outstanding questions regarding the biogeography and conservation of phylogenetic and trait diversity for several key reasons. A long history of intense research due to their visibility and popularity means they are perhaps the most well studied group of tetrapods. As a result, high quality data is plentiful for the vast majority of species with regards to their distribution, morphology, ecology, and evolutionary relationships (Cooney et al., 2017; Jetz et al., 2012; Orme et al., 2005; Tobias et al., 2022; Wilman et al., 2014). Birds are a large, ecologically diverse group, that have evolved to exploit nearly all terrestrial land masses and environmental conditions. Furthermore, they exhibit a remarkable range of phenotypes, such as those related to their ecological niches (Pigot et al., 2016) (e.g., bill shape; **Figure 1.4**), making them an ideal group to study biogeographical variation in morphological diversity (Pigot et al., 2020; Sheard et al., 2020). To capture this variation, robust trait data are essential. Recent advances in the collection of morphological data have resulted in exceptionally high-quality, continuous trait

data (Tobias et al., 2022; Wilman et al., 2014), including 3D beak shape data (Cooney et al., 2017; Hughes et al., 2022), for the entire class. Furthermore, the evolutionary history of birds is well researched, with a well-resolved phylogenetic super tree for the whole radiation (Jetz et al., 2012) and large amounts of genetic information available for many species which are increasing all the time (Feng et al., 2020), facilitating the calculation of phylogenetic diversity metrics.

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Figure 1.4: Diversity of bill morphology in the Malagasy Vangas (Vangidae). Species pictured bottom-left to top-right: Nuthatch Vanga (*Hypositta corallirostris*), Blue Vanga (*Cyanolanius madagascariensis*), White-headed Vanga (*Artamella viridis*), Bernier's Vanga (*Oriolia bernieri*), Helmet Vanga (*Euryceros prevostii*) and Sickle-billed Vanga (*Falculea palliata*). Specimens from the skins collection at the Natural History Museum, Tring.

Like all species, birds face many threats from anthropogenic activities (e.g., logging, pollution, hunting, climate change, invasive species spread), with the biggest drivers of bird species decline thought to come from land-use change such as agricultural expansion (Harfoot et al., 2021; Laurance et al., 2014). Birds carry out many important functions and ecosystem services that are of benefit to humanity (e.g., seed dispersal, disease control) that are at risk of being lost due to species extinctions (Şekercioğlu et al., 2016). The risk of extinction is not equal across the avian class, or between different morphological groups of species (Lee and Jetz, 2011; Ripple et al., 2017). Individual bird species threat status' have been classified extensively under the International Union for Conservation of Nature (IUCN) Red List of Threatened Species, making them an ideal group to assess the impacts of species loss on the ecological and evolutionary components of biodiversity. In summary, birds are prominent and ecologically important components of ecosystems with plentiful, detailed data regarding their phylogenetic relationships, traits, distributions, and threat statuses available, making them the ideal taxa to investigate extant and future patterns of phylogenetic and morphological biodiversity.

1.8 Thesis overview

In this thesis, I address several key knowledge gaps regarding the biogeographic patterns of extant avian morphological diversity, and how patterns of morphological and phylogenetic diversity will change in the face of global change. To do this, I use species geographic, morphological, phylogenetic and threat status data for most of the worlds bird species.

In Chapter 2, *Global biogeographic patterns of avian morphological diversity*, I map global patterns of avian morphological diversity and test for ecological and evolutionary drivers of extant patterns of morphological diversity.

In Chapter 3, *The homogenisation of avian morphological and phylogenetic diversity under the global extinction crisis*, I examine whether the extinction of sequential IUCN threat categories (Critically Endangered – Vulnerable) leads to morphological and phylogenetic homogenisation across the entire bird class, and biome and ecoregion assemblages across the globe.

Chapter 4 *The effects of tropical secondary forest regeneration on avian phylogenetic diversity* moves from a global macroecological perspective to a more local, conservation-focused perspective. It focuses on the potential recovery of pan-tropical secondary forest bird communities. Here, I primarily investigate if and how phylogenetic diversity recovers in secondary forests as time since disturbance and distance to primary forest increases.

In Chapter 5, I draw together the main findings of the thesis and offer thoughts and discussion on implications and further areas of research.

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CHAPTER 2

Global biogeographic patterns of avian morphological diversity.

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A PDF of the Ecology Letters manuscript is provided at the end of this Thesis in the Key Publication section.

2. 1 Abstract

Understanding the biogeographical patterns, and evolutionary and ecological drivers, underpinning morphological diversity are key for determining its origins and conservation. Using a comprehensive set of continuous morphological traits extracted from museum collections of 8353 bird species, including geometric morphometric beak shape data, we find that avian morphological diversity is unevenly distributed globally, even after controlling for species richness, with exceptionally dense packing of species in hyper-diverse tropical hotspots. At the regional level, these areas also have high morphological variance, with species exhibiting high phenotypic diversity. Evolutionary history likely plays a key role in shaping these patterns, with evolutionarily old species contributing to niche expansion, and young species contributing to niche packing. Taken together, these results imply that the tropics are both 'cradles' and 'museums' of phenotypic diversity.

2.2 Introduction

Exploring and understanding global patterns of biodiversity is central for determining its origins and conservation. Numerous hypotheses have been posited to explain how biodiversity has accumulated over geographical space and evolutionary time, with particular focus on how species richness varies across major environmental gradients (MacArthur 1965; Rohde 1992; Currie *et al.* 1999; Gaston 2000). However, species richness-based metrics of diversity consider all species as equal units, ignoring differences among species in their evolutionary history, morphology, or ecological roles, and do not adequately explain community structure or the mechanisms underlying species coexistence (Faith 1992; Purvis & Hector 2000; Stevens *et al.* 2003; Devictor *et al.* 2010; Safi *et al.* 2011). One approach to combating these shortfalls is to classify species according to their functional roles (e.g. diet, behaviour or life history), allowing investigation into how species are structured within communities, and the potential historical, environmental and ecological drivers leading to spatial variation in community assembly (Safi *et al.* 2011; Belmaker *et al.* 2012).

An alternative to classifying species into functional groups based on scoring of functional roles is to use continuous morphological traits to capture ecologically relevant variation (Jones *et al.* 2009; Wilman *et al.* 2014; Pigot *et al.* 2016a; Oliveira *et al.* 2017; Pigot *et al.* 2020; Kohli & Jarzyna 2021; McLean *et al.* 2021). This is beneficial where behavioural observations are lacking or unavailable for rare or cryptic species, across large geographical scales and for whole taxonomic groups. More generally, recent simulation studies have shown that using coarse grained data can be misleading in studies of species community or assemblage structure and recommend the use of high-resolution continuous data where possible (Kohli & Jarzyna 2021). Such detailed morphological trait data can capture variation among

functional categories (Pigot *et al.* 2020), providing fine-grained resolution that distinguishes multiple morphologies filling a single functional role and avoids the need to assign species to functional categories. The advent of novel, high-quality datasets of morphological traits for entire classes has advanced understanding of how communities fill multidimensional trait space (i.e. morphospace) (Pigot *et al.* 2016a), how morphological form maps to ecological role and/ or function (Anderson *et al.* 2011; Bright *et al.* 2016, 2019; Miller *et al.* 2017; Olsen 2017; Navalón *et al.* 2019; Pigot *et al.* 2020), and how morphological diversity has evolved and is distributed across the phylogeny (Cooney *et al.* 2017). Nonetheless, with a few exceptions (Sheard *et al.* 2020; McLean *et al.* 2021), we lack good understanding of the biogeographical patterns of morphological diversity at a global scale, and thus of the macroecological factors driving trait diversity both within and across species assemblages. In this study we use continuously measured morphological traits as a high-resolution approximation of the diversity of ecological roles.

Communities vary in terms of their species richness, and this variation may be associated with ecological 'niche packing' and/or 'niche expansion' (MacArthur 1965; Karr & James 1975; Pigot *et al.* 2016a). The packing of niche space occurs due to the finer specialisation of phenotypes or increased overlap in resource use, leading to increased density of species in morphospace over a smaller volume (MacArthur 1965; Karr & James 1975; Pigot *et al.* 2016a). Alternatively, species may fill an expanded variety of niches and exhibit dissimilar morphologies, revealed by higher volumes and lower densities of species in morphospace (Pigot *et al.* 2016a). Investigating how species fill morphospace in terms of both the volume and density occupied can therefore inform on the species richness of communities.

Variation in communities' morphological diversity results from a combination of evolutionary and environmental factors that have shaped global patterns of biodiversity accumulation (Safi *et al.* 2011), leading to the prediction that avian morphological diversity will be distributed unevenly across the globe. For instance, in heterogeneous habitats, species are likely to coexist due to greater availability of niches (MacArthur & MacArthur 1961; Kerr & Packer 1997; Guégan *et al.* 1998; Kerr *et al.* 2001; Rahbek & Graves 2001), and we therefore predict that assemblages will occupy morphospace at higher density than in homogeneous habitats. Habitats are also expected to vary with altitude (Kerr & Packer 1997; Rahbek & Graves 2001; Davies *et al.* 2007), with mountainous regions forming important dispersal barriers, centres for recent speciation, and exhibiting high species richness (α-diversity) and turnover (β-diversity) across entire montane slopes (Davies *et al.* 2007; Graham *et al.* 2009; Melo *et al.* 2009; Voskamp *et al.* 2017; Jarzyna *et al.* 2021). We expect to find high morphological density, with species filling similar areas in trait space, in areas transcending the largest altitudinal ranges (i.e. mid-montane slopes) due to the packing of niche space of closely related species, both before, and after controlling for species richness.

The influence of ecological limits to species coexistence may be reduced in areas of high productivity as resources are plentiful (Mittelbach *et al.* 2001; Pigot *et al.* 2016b), potentially supporting many species filling similar roles (i.e. niche packing) that are more finely specialised in their morphology. Equally, if resources are limited, communities may show low morphological density, with species needing to occupy wider ecological niches (Safi *et al.* 2011). Consequently, we predict the greatest morphological density in highly productive areas, and low morphological density where productivity is poor.

Evolutionary factors also influence the temporal accumulation of biodiversity. Over time, the divergence of species and their traits will shape the accumulation of phenotypic diversity in communities. Species that represent older, more isolated branches - i.e. those with higher evolutionary distinctness (Vane-Wright *et al.* 1991; Redding & Mooers 2006; Jetz *et al.* 2014) - may possess phenotypic traits that are unique and so fill otherwise unoccupied areas of trait space (Redding *et al.* 2010; Jetz *et al.* 2014). We predict that assemblages with high sums of evolutionary distinctiveness, and therefore representing more total evolutionary history, will have greater phenotypic diversity. These assemblages should contain species that are spread out in morphospace, leading to higher morphological volumes and lower morphological densities.

Here, we focus on testing these predictions in birds, which exhibit a huge diversity of phenotypes (Cooney *et al.* 2017; Pigot *et al.* 2020; Tobias *et al.* 2020), worldwide distribution across all terrestrial land-masses (Orme *et al.* 2005), and high-quality phylogenetic and trait data (Jetz *et al.* 2012; Wilman *et al.* 2014; Cooney *et al.* 2017). We use ecologically relevant morphological traits to: 1) map global patterns of avian morphological diversity; 2) identify areas with exceptional levels of morphological diversity; and 3) test the environmental and evolutionary drivers of global avian morphological diversity.

2.3 Materials and Methods

All data compilation, analysis and visualization were conducted in RStudio version 1.3.959 (RStudio Team 2020) and R version 4.0.2 (R Core Team 2020). We follow the taxonomy used in the BirdTree phylogeny http://birdtree.org/ (Jetz *et al.* 2012).

2.3.1 Morphological Trait Data

We compiled a dataset of continuous morphological traits that are linked to the ecological niches of birds in a community (Pigot *et al.* 2016a; Sheard *et al.* 2020).

2.3.1.1 Trait compilation

Using a 3D landmark-based beak shape dataset, we extracted coordinates for the bill shape for 8353 species of bird, across 189 (of 194) bird families. 3D scanning, post processing and landmarking were performed using protocols described in Chira *et al.* (2018) and Cooney *et al.* (2017). In summary, we took 3D scans of the beaks of museum study skins, using white and blue structured light scanning (*FlexScan3D*). For some families (e.g., nightjars [Caprimulgidae]), many species could not be scanned as they had feathers and/or bristles obscuring parts of the beak and are therefore underrepresented in our dataset (**Appendix 1 Figure S1**). From these scans, we used landmark-based geometric morphometric analysis to measure bill shape and ran a principal component analysis (PCA) to produce a morphospace capturing the major axes of bill shape variation (see Supporting Information, Section 1a for further information).

We extracted the first seven axes from the PCA, which accounted for 98.9% of the overall variation in bill shape (**Appendix 1 Figure S2, Table S1**). We calculated centroid size as a measure of bill size for each species in our dataset. For each specimen scanned, we took measurements of wing and tarsus length (mm). Where possible, if these measurements were not taken (e.g. broken tarsus, or sewn wings), another specimen, or a mean score calculated from multiple specimens was used. Body mass (g) for each species was taken from the EltonTraits database (Wilman *et al.* 2014). We include centroid size as well as body size

because there is substantial variation in beak size that cannot be explained by allometry alone (e.g. raptors, Bright *et al*. 2016).

2.3.1.2 Avian morphological trait space

Next, we constructed a raw morphological trait dataset containing the seven main axes of beak shape variation and combined them with $\log_{10}$-transformed measurements of body mass, centroid size, wing, and tarsus length. Trait data were centred and re-scaled by standardizing each to zero mean and unit variance (z-transformation). Finally, we ran a second PCA on this combined dataset and selected the first eight PC axes from the resultant morphospace which represented 96.1% of the variation in traits (**Figure 1, Appendix 1 Table S1**).

2.3.2 Spatial Data

Global distribution maps for all extant and probably extant bird species were obtained from BirdLife International (http://www.birdlife.org/datazone/home). Species breeding and resident range maps were included where these species were classified as native or re-introduced. Whilst these maps may be less accurate and do not incorporate abundance data as more focused surveys, they allow for a much broader scope, and analysis in regions where survey data is not available or sufficiently plentiful. Due to taxonomic differences, we first matched species names used by BirdLife to the BirdTree phylogeny http://birdtree.org/ (Jetz *et al.* 2012), and range maps were projected onto a 100 km x 100 km equal area grid under a Behrmann cylindrical equal-area projection (see Supporting Information for further detail). Species presence or absence in each terrestrial grid cell was recorded. Our final dataset comprised 8353/9993 (83.6%) species, distributed across 15980 assemblages. For each

assemblage, species lists and species richness were obtained. Global maps and phylogenetic plots of omitted species can be found in the Supporting Information (**Appendix 1 Figure S1, S3**).

2.3.3 Morphological Disparity Metrics

Numerous disparity metrics have been proposed to assess how species occupy multidimensional trait space. Using single metrics to quantify multidimensional space occupancy limits the ecological inferences that can be made (Villéger *et al.* 2008; Guillerme *et al.* 2020). Therefore, we aimed to select one metric that accurately captured changes in morphospace volume and another that captured changes in density (i.e. how species fill trait space).

To quantify and understand the potential for different metrics to capture such changes in volume and density, we used the function *test.metric* in the R package *dispRity* (version 1.5.0: Guillerme 2018), following protocols described by Guillerme *et al.* (2020). Based on simulations of species gains and loss, we selected the metrics i) sum of variance (Foote 1992), and ii) mean distance to nearest neighbour (i.e. the mean Euclidean distance between a species and its nearest neighbour: Foote 1992). The sum of variance is commonly used as a measure of volume, but it may also capture certain aspects of density (Guillerme *et al.* 2020) (e.g. a high number of species close to the mean trait value will reduce the sum of variance). Therefore, we define the sum of variance as a measure that captures the spread, or variance, of species in trait space (morphological variance). We decided against using a commonly used, alternative measure of volume, the sum of ranges (Foote 1992), as it is more sensitive to outliers (Guillerme *et al.* 2020). The mean distance to nearest neighbour quantifies the

density of species packing in morphospace (morphological density). Both metrics were calculated for each unique assemblage using the *dispRity* R package (version 1.5.0: Guillerme 2018).

2.3.4 Assemblage Evolutionary Distinctiveness

We downloaded 100 complete species-level phylogenetic trees based on the Hackett backbone (Hackett *et al.* 2008) from http://birdtree.org/ (Jetz *et al.* 2012). For each tree, we calculated an evolutionary distinctiveness score for each species in the phylogeny (n=9993), using the 'equal splits' derivation (Redding & Mooers 2006) in the *evol.distinct* function in the R package *picante* (version 1.8.2: Kembel *et al.* 2010). 'Equal splits' divides each branch length by the daughter species it represents, giving a value for each species of the amount of evolutionary time each embodies. For each community, evolutionary distinctiveness scores for all species present were summed. This was done for each of the 100 trees, and a mean value was taken giving an 'assemblage evolutionary distinctiveness' score for each community.

2.3.5 Null models

To test whether the morphological variance, density and assemblage evolutionary distinctiveness of each assemblage deviated from expected given the observed species richness, we constructed null models based on two different species pools. Firstly, we used a global species pool where any species from the entire dataset could be drawn. Secondly, we used a species pool where draws were restricted to phylogenetically distinct regional pools in order to avoid sampling from largely historically independent assemblages (**Appendix 1 Figure S4**). To do this, we followed the protocol outlined by Holt *et al.* (2013) and defined 13

unique phylogenetic regions that have distinct evolutionary histories (**Appendix 1 Section 1C**). Null models for each grid cell were calculated using both species pools, enabling us to capture regional effects under a global species pool, and more local effects when using a phyloregional species pool.

For each unique species richness value, 1000 null communities were generated and morphological variance and density were calculated. For each of the 100 sets of evolutionary distinctiveness scores, 1000 null communities were generated, and assemblage evolutionary distinctiveness was calculated. To assess the difference between the observed (variance, density, assemblage evolutionary distinctiveness) and simulated (null) biodiversity values, we calculated the standardised effect size (SES) for each assemblage: A positive SES value indicates a higher biodiversity value than expected based on null simulations, while a negative SES indicates a lower value. Exceptional values of morphological variance, density and assemblage evolutionary distinctiveness were those that showed statistically significant deviation from expected (+/- 2).

2.3.6 Environmental correlates

For each grid cell, we extracted environmental variables that we predicted are associated with geographical variation in morphological diversity: main habitat type (Buchhorn *et al.* 2020), the number of unique habitats (Shannon's index) (Buchhorn *et al.* 2020), altitudinal range (Fick & Hijmans 2017), and gross primary productivity (GPP) (Zhang *et al.* 2017a, b) (see **Appendix 1 Section S1D** for full details).

2.3.7 Predicting patterns of morphological diversity

We fitted generalised least squares (GLS) models using the function *gls* in the R package *nlme* (version 3.1-149: Pinheiro *et al.* 2020) with either morphological variance$_{SES}$ or morphological density$_{SES}$ (calculated using both global and phyloregional species pools) as response variables. Species richness, assemblage evolutionary distinctiveness$_{SES}$, GPP, habitat heterogeneity, altitudinal range, and habitat type were included in the full model as predictor variables, with additional models fitted where the categorical variable habitat type was dropped or included alone (**Appendix 1 Table S2**).

We log_{10}-transformed the variables species richness, GPP, habitat heterogeneity and altitudinal range. To allow for non-linear relationships between our response and predictor variables, we included both linear and quadratic terms of the numeric predictor variables in our models. To account for spatial autocorrelation, all models were fitted with either exponential, gaussian or spherical correlation structures, using spatial information from longitudinal and latitudinal cell centroid values. We used Akaike Information Criterion scores (AIC) to select the best-fitting models for each dependent variable, with the models with the lowest AIC scores considered to be most well supported (**Appendix 1 Table S2**). Due to computational limits, the 15277 terrestrial grid cells were split into 25% subsets using a chequerboard approach, where every fourth terrestrial grid cell was included (e.g. set A: 1,5,9… etc.). All models were run on each of the four subsets (**Appendix 1 Table S2**).

2.4 Results

2.4.1 Avian Morphospace

Variation in avian morphological traits is distributed such that the majority of species occupy a dense core in the centre, with more extreme forms found towards the edges of morphospace (**Figure 2.1, Appendix 1 Figure S2**) (Chira *et al.* 2018; Pigot *et al.* 2020). When considering all morphological traits together, 96% of the variation is captured by 8 PCs (**Figure 2.1**). PC1 (35% variation) is dominated by size metrics, describing the spectrum from the largest (e.g. cranes [Gruidae]) to smallest (e.g. hummingbirds [Trochilidae]) species.

The major axis of beak shape primarily loads onto the second PC of morphological trait variation, with long pointed bills (e.g. sword-billed hummingbird [*Ensifera ensifera*]) to short, wide beaks (e.g. swifts [Apodidae]). Certain groups of species occupy distinct areas of morphospace that are only apparent on PC axes that themselves account for low total variation, such as waterfowl (Anseriformes) on PCs 5 and 6, and flamingos (Phoenicopteriformes) on PC7 and PC8.

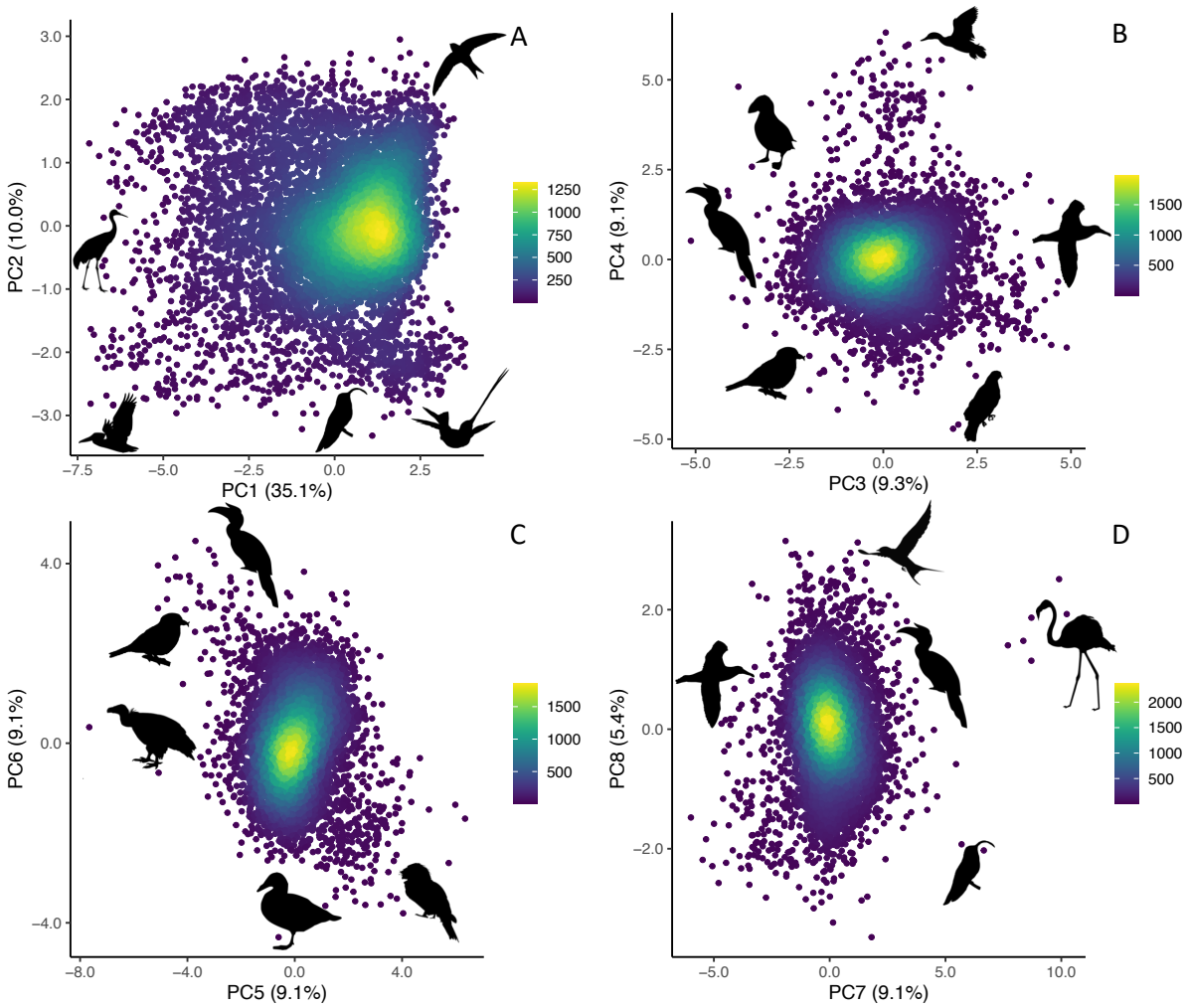


Figure 2.1: Scatterplots showing the first 8 principal components of morphological traits, and the proportion of variance represented by each. The scale bar shows the number of neighbouring points within one standard deviation of the Euclidean distance of each species to all other species across both axes for each scatterplot. Points were coloured with yellow being where species are most numerous, and purple least numerous. PC1 is dominated by size metrics, with high values corresponding to small body mass, tarsus, wing, and bill (centroid) size, and the largest species falling at negative values. PC2 captures the main variation of beak shape, going from long, pointy bills at the negative end of the spectrum, to wide, short bills at the positive end. The remaining PCs capture more nuanced variation in beak shape (**Appendix 1 Figure S2**). All silhouettes are in the public domain and were downloaded from PhyloPic.org.

2.4.2 Global distributions of morphological diversity.

Avian morphological diversity is unevenly distributed globally (**Figure 2.2**). New Zealand, Patagonia, and the Atacama Desert contain assemblages with high values of morphological variance, where species occupy large areas of trait space. Low values of morphological variance are found along the species-rich mountain ranges of the Himalayas and Andes, and the species-impoverished Sahara and Arabian Peninsula (**Figure 2.2A**). Areas around the Sahara and Arctic contain communities where nearest neighbour distance is high, suggesting low morphospace density. Assemblages containing species that are particularly clustered in morphospace (high morphospace density) are found along the Andean and Himalayan mountains, African rift valley, and some oceanic islands (**Figure 2.2B**).

Communities with the highest assemblage evolutionary distinctiveness are found in the Neotropics, particularly along the Andes and Amazonian basin, African Rift Valley, and Himalayas. Low assemblage evolutionary distinctiveness occurs across the Saharo-Arabian belt, polar regions, and island archipelagos (**Appendix 1 Figure S5B**). Overall, spatial patterns of the raw metrics suggest a relationship with species richness (**Figure 2.3, Appendix 1 Figures S5A, S6**) with, for example, the lowest morphological densities occurring in areas of low species richness (**Figure 2.2B**) and the highest assemblage evolutionary distinctiveness communities being those with high species richness (**Appendix 1 Figure S5B**).

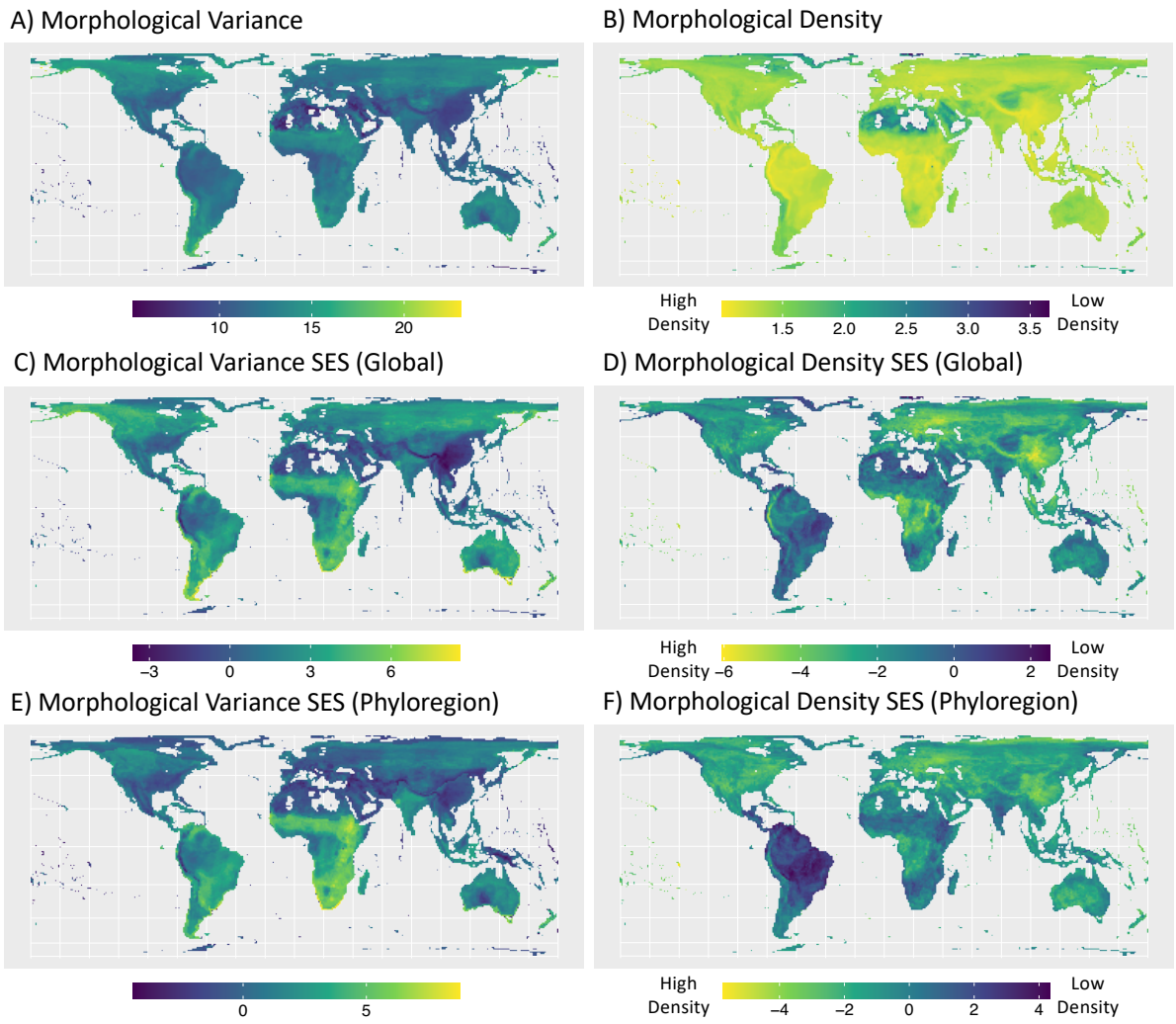


Figure 2.2: A) Morphological variance (sum of variances) and B) morphological density (mean nearest neighbour distance) for 8352 bird species across 15980 terrestrial 1 degree grid cells under Behrmann projection. Standard effect sizes (SES) for each variable were calculated from global (C, D) and phyloregional (E, F) species pools.

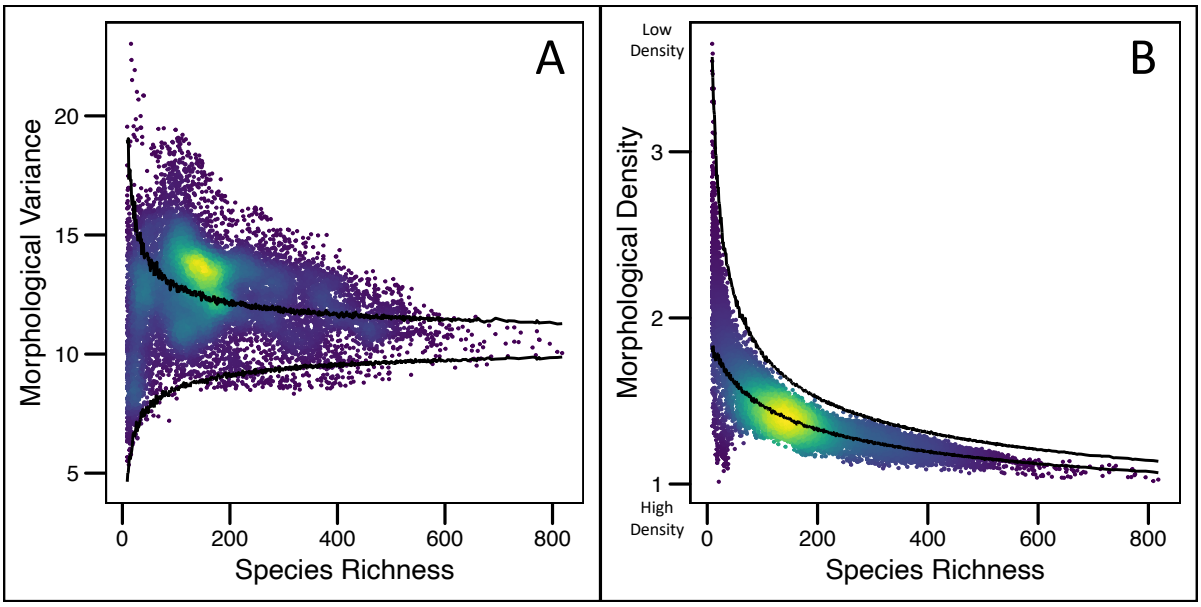


Figure 2.3: Scatter plots showing the relationship between species richness and A) morphological variance (sum of variances), and B) morphological density (mean nearest neighbour distance). Points are coloured according to the number of neighbouring points present to highlight where species are most numerous, with yellow the most and purple the least numerous. The lines show the upper (97.5) and lower (2.5) quantiles calculated across null communities drawn from a global species pool for each value of species richness.

2.4.3 Geographic distribution of exceptional morphological diversity.

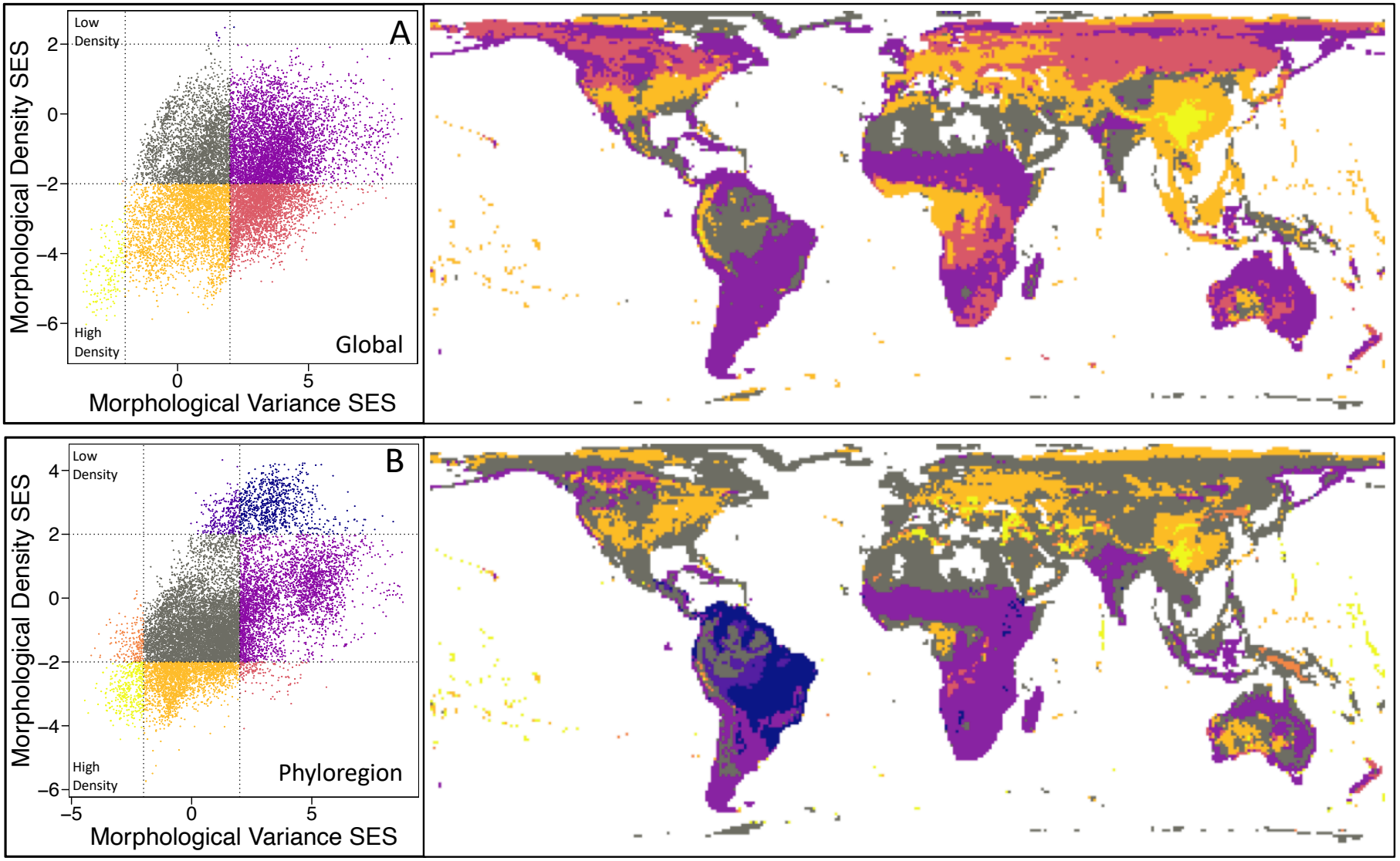
Observed morphological variance tends to be greater than expected (**Figure 2.3A**) for both global, and to a lesser extent for phyloregional pools (**Appendix 1 Figure S7**). These deviations from expectation show strong spatial patterns. We find higher than expected morphological variance along the South American and South Australian coastlines, and in East and South Africa, when using both global and phyloregional pools, highlighting wider assemblage niche breadths (**Figures 2.2C, E**). Differences between the species pools arise in the mountains of New Guinea, where morphological variance is much lower than expected using a phyloregional pool, but not a global pool (**Figures 2.2C, E**).

Morphological density tends to be greater than expected under a global pool (**Figure 2.3B**), but similar to expected when using phyloregional pools (**Appendix 1 Figure S8**). Spatially, we find that for both global and phyloregional species pools, the Andes harbour morphologically dense communities, with species that are more clustered in trait space than expected given species richness (**Figures 2.2D, F**). Under a global pool, species occupy morphospace less densely than expected across small areas of the South American lowland tropics, with this pattern extending over greater areas under a phyloregional pool (**Figures 2.2D, F**).

We find slightly lower than expected values of assemblage evolutionary distinctiveness for both global and phyloregional null models (**Appendix 1 Figures S5C, S5D, S6, S9**). Under a global species pool, assemblages in the tropics and Southern Hemisphere are more evolutionarily distinct than expected based on null simulations, with hotspots in Madagascar, Borneo, tropical central Africa, etc. (**Appendix 1 Figure S5C**). The Andes contain much lower assemblage evolutionary distinctiveness than expected, with younger lineages and/or close relatives dominating (**Appendix 1 Figure S5C**). Patterns are similar under phyloregional pools, but with Australasian assemblages showing expected, rather than greater, assemblage evolutionary distinctiveness (**Appendix 1 Figure S5D**).

We identified areas with combinations of exceptional (+/- 2 s.d) morphological variance, morphological density or assemblage evolutionary distinctiveness. Using global species pools, we find dense packing of species and expected (or lower than expected) variance in SE Asia, tropical West and Central Africa, as well as along the highest terrestrial mountain ranges, the Andes and Himalayas, showing that high richness areas are prone to niche packing (**Figure 2.4A**). The Northern Hemisphere is characterised by expected assemblage evolutionary

distinctiveness, with species filling expected or high volumes of morphospace, whilst having close neighbours present (**Appendix 1 Figures S10A, C**). Under a phyloregional pool, the Central Highlands of New Guinea are one of few areas in tropical regions with lower morphological variance than expected (**Figure 2.4B**), with the western part of the range showing greater assemblage evolutionary distinctiveness than expected, highlighting it as an area with older lineages that are filling similar niches (**Appendix 1 Figure S10B, D**). Oceanic islands tend to hold assemblages with species clustered in smaller volumes of trait space than expected, with many (i.e Galapagos etc.) also containing species representing greater than expected evolutionary distinctiveness (**Appendix 1 Figure S10B, D**).


A
Low
Density
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Density
Global
Morphological Density SES
Morphological Variance SES
2
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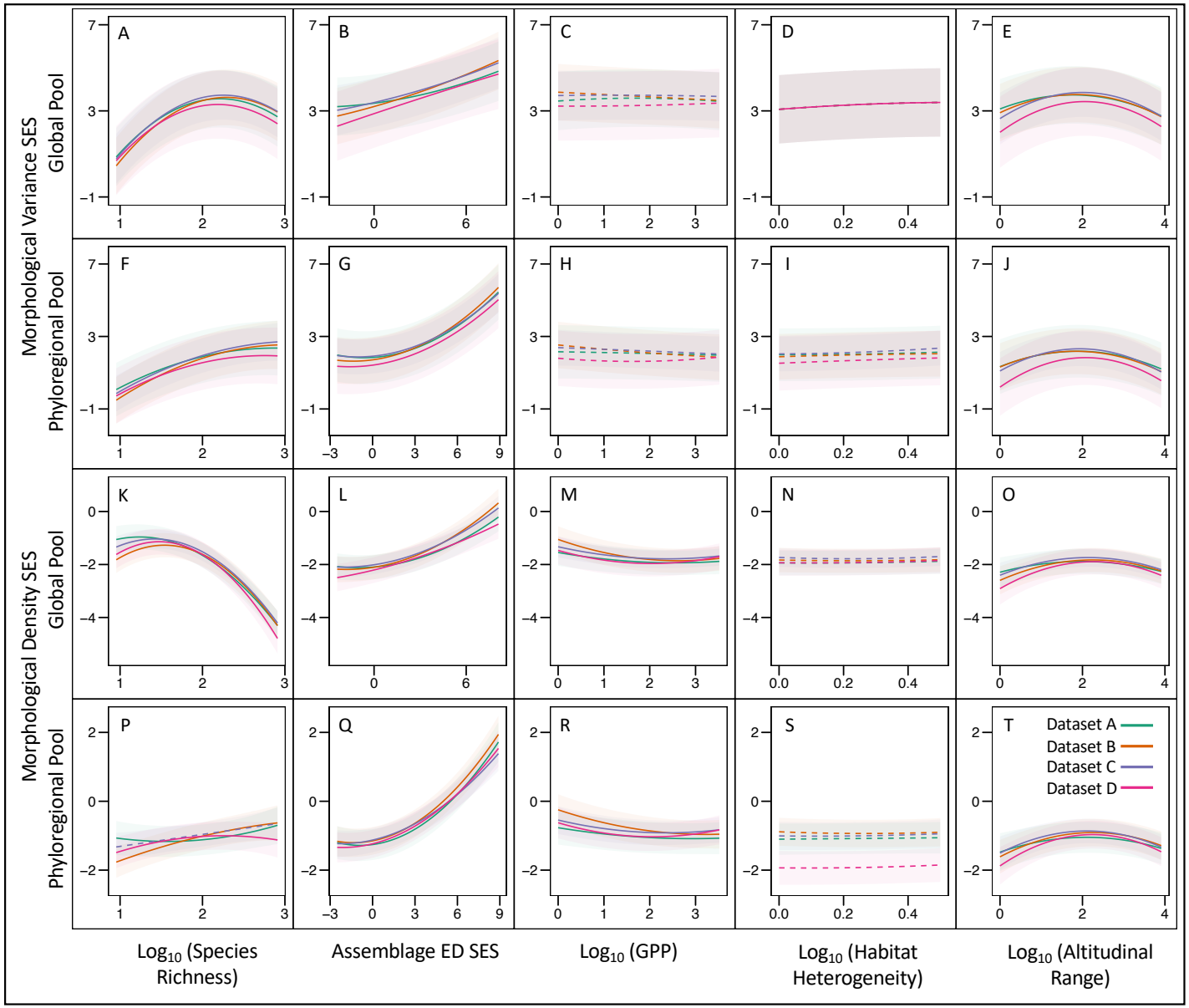
High
Density
Phyloregion
Morphological Density SES
Morphological Variance SES
4
2
0
−2
−4
−6
−5
0
5

Figure 2.4: Areas of the globe where the standard effect sizes (SES) of different biodiversity metrics (morphological variance (sum of variances) and morphological density (mean nearest neighbour distance)) show statistically significant deviation from expected (+/- 2) for 8352 bird species across 15980 terrestrial 1 degree grid cells under Behrmann projection. Combinations of variables are A) morphological variance$_{SES}$ and morphological density$_{SES}$ where SES was calculated using global species pools, and B) using phyloregional species pools. The grey colour shows no significant deviation from expected.

2.4.4 Environmental and evolutionary drivers of morphological diversity.

Morphological variance$_{SES}$ (MV_{SES}) is associated with species richness, assemblage evolutionary distinctiveness$_{SES}$, and altitudinal range, but not with gross primary productivity (GPP), habitat heterogeneity, and habitat type (**Appendix 1 Table S2**). Global-pool MV_{SES} increases strongly before plateauing and subsequently declining with increasing species richness ($p<0.001$: **Figure 2.5A, Appendix 1 Table S3**), suggesting a pattern of morphospace expansion followed by packing at high species richness. MV_{SES} increases linearly with increasing evolutionary distinctiveness$_{SES}$ with the linear term ($p<0.001$) and not the quadratic term ($p>0.05$) significant (**Figure 2.5B, Appendix 1 Table S3**). MV_{SES} initially increases with altitudinal range from low (e.g. lowland plains, upland plateaus) to mid-elevational ranges before decreasing to lower levels where elevational range is greatest (e.g. montane slopes) ($p<0.001$: **Figure 2.5E, Appendix 1 Table S3**). We find no association between MV_{SES} and GPP, and an almost flat relationship with habitat heterogeneity for just one subsample of our data (dataset D) ($p<0.01$ (linear term only): **Figure 2.5D, Appendix 1 Table S3**). Overall, we find broadly similar results when calculating phyloregional-pool MV_{SES} (**Figure 2.5F-J, Appendix 1 Table S3).**

Morphological density$_{SES}$ (MD_{SES}) is also associated with species richness, assemblage evolutionary distinctiveness$_{SES}$, altitudinal range and GPP, but not habitat heterogeneity or habitat type (**Appendix 1 Table S2**). We find an initially flat relationship between global-pool MD_{SES} and species richness, before distances between species sharply decrease as species richness increases ($p<0.001$: **Figure 2.5K, Appendix 1 Table S3**). Overall, we find a positive relationship between MD_{SES} and assemblage evolutionary distinctiveness$_{SES}$, with species most spread out in trait space where assemblages have the highest assemblage evolutionary distinctiveness given species richness ($p<0.05$: **Figure 2.5L, Appendix 1 Table S3**). Species pack more closely in trait space than expected as energy availability (GPP) increases ($p<0.05$: **Figure 2.5M, Appendix 1 Table S3**). Assemblages are most packed at flat (e.g lowland plains, upland plateaus) and steep (mid-montane slopes) elevational ranges, with species most spread out at mid-elevational ranges ($p<0.01$: **Figure 2.5O, Appendix 1 Table S3**). No relationship between MD_{SES} and habitat heterogeneity was found (**Appendix 1 Table S3**). Under phyloregional pools, we find a contrast in model outputs where species richness is the predictor variable. As species richness increases, species become slightly less clustered in trait space than expected when using datasets B and D ($p<0.01$ (linear term only)), but for dataset A, we find species are most clustered in trait space (low MD_{SES}) at mid species richness values ($p<0.05$) (**Figure 2.5P, Appendix 1 Table S3**).


Morphological Variance SES
Global Pool
Phyloregional Pool
Morphological Density SES
Global Pool
Phyloregional Pool
A
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Q
R
S
T
Dataset A
Dataset B
Dataset C
Dataset D
Log10 (Species Richness)
Assemblage ED SES
Log10 (GPP)
Log10 (Habitat Heterogeneity)
Log10 (Altitudinal Range)

Figure 2.5: The effect of species richness, assemblage evolutionary distinctiveness (sum of equal splits) SES, gross primary productivity (GPP), habitat heterogeneity (Shannon's index), and altitudinal range on morphological variance (sum of variances) SES (generated from global (A-E) and phyloregional species pools (F-J)), and on morphological density (mean nearest neighbour distance) SES (generated from global (K-O) and phyloregional species pools (P-T)). High values of morphological density represent high mean nearest neighbour distances and therefore low density. Low values of morphological density represent low mean nearest neighbour distances and so high density. All raw variables (i.e. non-SES) are on a $\log_{10}$ scale. The lines represent predicted relationships from the multiple predictor gls models, with solid lines representing significant predictors whereas dotted lines are non-significant. Colours correspond to each 25% data subset (Dataset A = green, B = orange, C = purple, and D = pink).

2.5 Discussion

We present the first global mapping of a comprehensive set of continuous morphological traits, including three-dimensional bill shape data, for 8353 bird species, revealing regions of the world with exceptional relative spread and density of species traits. Our results suggest large-scale geographic variation in the relative importance of niche expansion and niche packing. Density and variance of morphological trait distributions scale with species richness and evolutionary distinctiveness, whereas only density scales with productivity (albeit weakly). Taken together, we suggest that evolutionary history plays a key role in shaping assemblage composition, particularly through niche expansion, whereas contemporary environment contributes more to niche packing.

Our use of global and phyloregional pools reveals the broad role of evolutionary history in shaping global assemblage structure. Tropical biodiversity hotspots, including the highland tropical Andes (Jarzyna *et al.* 2021), much of the central African tropics, and Indo-Malayan archipelago are densely packed compared to the global pool but not when compared to

phyloregional faunas. In the same regions, variance follows global expectations but is higher than expected under the phyloregional null model. Such patterns would be expected if these hyper-diverse regions are both 'museums' where old species persist, and 'cradles' of diversity, where speciation rates are high (Gaston & Blackburn 1996; Jablonski *et al.* 2006; McKenna & Farrell 2006; Rolland *et al.* 2014). For instance, if morphological divergence is closely related to species age, surviving lineages will lead to greater morphospace volumes, and in addition, high numbers of closely-related young species will cause the denser packing of niche space in the tropics. In contrast, oceanic islands retain high density irrespective of the species pool. Collectively these patterns imply a lasting imprint of distinct evolutionary and biogeographic histories on assemblage structure.

Areas of the Northern temperate regions tend to be more densely packed than expected, mirroring findings from smaller areas in the temperate lowlands using mostly categorical traits (Jarzyna *et al.* 2021). We also find a tendency for temperate assemblages to have higher morphological variance than expected under a global pool null model. Although it is difficult to directly infer the ecological drivers of community assembly using cell assemblage-based methods alone (Blanchet *et al.* 2020), our results hint that habitat filtering may contribute more to temperate, especially Northern Hemisphere regions, in shaping assemblage structuring. The observed pattern can only arise if morphospace is occupied by clusters of morphologically similar species, but where these clusters are spaced apart from one another. This would lead to high density within clusters, and high variance (the clusters are spread out across morphospace). This observation fits previous findings that standardised mean distance to centroid (functional dispersion) is greatest for birds in temperate and polar biomes (Cooke *et al.* 2019). Communities in the temperate and polar regions contain many species that

migrate south during the Northern winter, with the remaining species likely to possess combinations of traits that allow survival over the harsh winter months (e.g. ecological guilds such as granivores and scavengers: Carnicer & Díaz-Delgado 2008) leading to increased niche packing in these areas of morphospace.

The importance of evolutionary history for assemblage structure is further supported by our analyses of predictors of morphological diversity. Morphological diversity is expected to correlate strongly with species richness (Safi *et al.* 2011), as adding species must increase either volume or density. However, even after controlling for species richness using null models, we still find that species richness is a strong predictor of both morphological density and volume. Compared to both global and phyloregional models, morphological volume increases with species richness, suggesting niche expansion, before plateauing at high levels of species richness. This leads to increasing functional redundancy in species-rich regions (Oliveira *et al.* 2016). In contrast, and only for global models, niche space is exceptionally densely packed in areas of high species richness. This implies that niche packing becomes dominant in hyper-diverse assemblages, and mirrors findings that the similarity of bird species functional roles is highest in species-rich areas (Cooke *et al.* 2019).

Alongside species richness effects, we also find that assemblages with greater than expected evolutionary distinctiveness have both high variance and lower density in morphological space. This is consistent with the expected link between phylogenetic diversity and morphological diversity (Faith 1992; Safi *et al.* 2011; Mazel *et al.* 2018) and suggests that niche expansion reflects phylogenetic history and the presence of more evolutionarily distinct species in hyper-diverse assemblages. In contrast, the combined increase in density with

richness but decline with evolutionary distinctiveness implies that the packing of species in hyper-diverse assemblages is not a reflection of time since divergence. Instead, density, but not volume, increases with productivity. We suggest that assemblage morphospace expansion is driven by the accumulation of evolutionarily old lineages whereas packing is potentially the result of stable and productive environments supporting morphologically similar and evolutionarily young species. However, we note that the effects of productivity on morphological diversity are comparatively weak and therefore this interpretation ought to be treated with caution.

In addition to evolutionary history and productivity, we find some support for the expectation that heterogeneous habitats contain more niches, and can support morphologically more similar species, than homogenous ones (Kerr *et al.* 2001; Rahbek & Graves 2001). As altitudinal range increases, morphological density decreases, and volume increases, as species fill more niches resulting in a peak at mid-altitudinal ranges. The subsequent decline of morphological volume and increasing morphological density as species cluster in trait space at high altitudinal ranges (i.e. mid-montane slopes), is likely attributable to the high richness (α-diversity) (e.g. Davies *et al.* 2007) and turnover (β-diversity) (Graham *et al.* 2009) of closely related species (Voskamp *et al.* 2017), characteristic of such areas.

In our study, trait data were not available for all species, and biases in sampling could exist both phylogenetically and spatially (Figure S1 & Figure S3) (Etard *et al.* 2020). For instance, certain groups, particularly those with rictal bristles or feathers obscuring the bill (e.g. nightjars and allies [Caprimulgiformes] (**Figure 2.6**)), are under-represented because we were not able to obtain complete 3D bill scans. Globally, assemblages contain an average of 94%

of species, with no assemblage containing less than 70% of species. Spatially, high richness areas are more likely to contain the greatest numbers of species with missing trait data, although these tend to be species from represented families with similar morphologies. We suggest, based on the phylogenetic (**Appendix 1 Figure S1**) and spatial (**Appendix 1 Figure S3**) structure of the missing data, that our analyses are unlikely to be strongly biased by missing data. We also suggest that the most likely impact of missing data is an underestimation of niche packing in high richness areas and a weaker relationship with productivity, although this is untested.

Figure 2.6: European Nightjar (*Caprimulgus europaeus*) showing rictal bristles around the beak. 20th April 2022, Romania.

In conclusion, our work reveals novel insights into the structure and drivers of avian assemblages. We argue that evolutionary history plays a key role in shaping assemblage structure notably with evolutionarily old species contributing to niche expansion, and evolutionarily young species contributing to niche packing in the tropics. We further suggest

that tropical niche packing is facilitated by high productivity and potentially, though not directly tested here, the long-term stability of the tropics.

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CHAPTER 3

The homogenisation of avian morphological and phylogenetic diversity under the global extinction crisis.

3.1 Abstract

Biodiversity is facing a global extinction crisis that will reduce ecological traits, evolutionary history, and ultimately ecosystem functioning and services. A key question in understanding how species losses will impact morphological and phylogenetic diversity at global scale. Here, we test whether the loss of species threatened with extinction according to the IUCN leads to morphological and phylogenetic homogenisation across both the whole avian class, and each biome and ecoregion globally. To do this, we use a comprehensive set of continuous morphological traits extracted from museum collections of 8455 bird species, including geometric morphometric beak shape data, and sequentially remove species from those at most to least threat of extinction. We find evidence of morphological, but not phylogenetic, homogenisation across the avian class, with species becoming more alike in terms of their morphology. We find that most biome and ecoregions are expected to lose morphological diversity at a greater rate than predicted by species loss alone, with the most imperilled regions found in East Asia, particularly the Himalayan uplands and foothills. Only a small proportion of assemblages are threatened with phylogenetic homogenisation, in particular parts of Indochina, such as Cambodia and Vietnam. Species extinctions will lead to a major loss of avian ecological strategies, but not a comparable loss of phylogenetic diversity. As the decline of species with unique traits and their replacement with more widespread generalist species continues, the protection of assemblages at most risk of morphological and phylogenetic homogenisation should be a key conservation priority.

3.2 Introduction

We are in the midst of a global extinction crisis, with biodiversity in the Anthropocene declining at an alarming rate (Barnosky et al., 2011; Dirzo et al., 2014). Biodiversity loss is often measured in terms of species richness decline, yet this does not always adequately capture the potential loss of unique ecological forms, traits, and evolutionary history that each species represents (Devictor et al., 2010; Faith, 1992; Purvis and Hector, 2000). Furthermore, at risk species may perform important ecological roles within communities with their loss leading to a decline in the diversity of ecological functions, including those currently important to humans as ecosystem services and those whose benefits are not currently realised (Dirzo et al., 2014; Faith, 1992; Hooper et al., 2005). To capture this, two groups of biodiversity metrics are increasingly measured: trait-based diversity (e.g., functional or morphological diversity) that aims to measure traits that enable species to occupy and function in an ecosystem (Petchey and Gaston, 2002; Tilman, 2001), and phylogenetic diversity, which quantifies the total amount of evolutionary history or feature diversity represented by all species in a community (Faith, 1992; Webb et al. 2002).

Both biodiversity measures are amassed over long evolutionary timespans and are often considered to be positively correlated (Wiens and Graham, 2005). This occurs where trait evolution is phylogenetically constrained such that species traits exhibit strong phylogenetic signal and diverge at a constant rate over time (i.e., following Brownian motion (Felsenstein, 1985)) (Felsenstein, 1985; Wiens and Graham, 2005). Therefore, the extinction of an evolutionarily old species with no close relatives that has evolved unique traits could have a greater impact on phylogenetic and trait diversity than a more recently evolved species with many close relatives with similar trait values (Oliveira et al., 2020; Redding et al., 2010).

However, not all species traits evolve and accumulate at a constant rate (e.g. (Chira and Thomas, 2016; Harmon et al., 2010; O'Meara et al., 2006; Venditti et al., 2011) or show strong phylogenetic signal (Losos, 2008). The relationship between phylogenetic and trait diversity can deviate and is therefore an intensely debated topic (Kelly et al., 2014; Mazel et al., 2018; Pavoine et al., 2013; Redding et al., 2010). Whilst the correlation between the two metrics strengthens as the number of traits measured increases (Tucker et al., 2018), it is impossible to quantify all traits that enable a species to exist in its niche and interact with its ecosystem. Phylogenetic diversity is well established as a tool that is expected to capture feature diversity more effectively than subsets of measurable traits (Faith, 2008, 1992). Conserving phylogenetic diversity can also protect biodiversity 'option-value', whereby currently unrealised benefits of biodiversity are protected for future generations (Faith, 1992). Recent studies have therefore moved towards measuring the impact of extinction on both phylogenetic and trait diversity in complement (e.g. (Brodie et al., 2021; Cooke et al., 2019; Oliveira et al., 2020).

Assessing the impact of extinction on both evolutionary and ecological components of biodiversity can reveal patterns of loss that cannot be understood by considering species loss alone. This is because these measures are particularly sensitive to the non-random loss of species (Cardillo et al., 2005) and can highlight where loss off threatened species could lead to biotic homogenisation (Clavel et al., 2011; Daru et al., 2021; McKinney and Lockwood, 1999). Extinction risk is not equal across the tree of life and between functional groups of species (Cardillo et al., 2008; Dirzo et al., 2014; Lee and Jetz, 2011; Ripple et al., 2017). For example, extinction over the next 100 years is predicted to lead to an ecological down-sizing of species, where the largest, most slow-lived species are lost (Cooke et al., 2019).

Furthermore, the current declines of frugivores can have major consequences for seedling dispersal and recruitment and therefore forest carbon storage (Bello et al., 2015; Brodie et al., 2021; Chanthorn et al., 2019; Rogers et al., 2021), and a paucity of large scavengers, for example vultures (the most threatened group of birds), could lead to disease outbreaks from carcasses (Buechley and Şekercioğlu, 2016; DeVault et al., 2016). Species at risk of extinction also tend to be phylogenetically clustered and overrepresented in particular groups (Purvis et al., 2000), as well as belonging to evolutionarily unique lineages (Murali et al., 2021; Vamosi and Wilson, 2008), increasing the likelihood that evolutionary history will be lost at an uneven rate across the tree of life (Purvis et al., 2000). At a global scale we predict that the loss of threatened species will lead to an overall homogenisation such that species trait and phylogenetic diversity is lost at a greater rate than expected through species loss alone.

The patterns of trait and phylogenetic homogenisation are also likely to vary across space. Firstly, raw phylogenetic and trait diversity are distributed unequally globally due to various abiotic and biotic factors (Hughes et al., 2022; McLean et al., 2021; Safi et al., 2011; Sheard et al., 2020; Voskamp et al., 2017). Secondly, threats faced (e.g., habitat loss, hunting, climate change) and species sensitivities to these threats are spatially variable and increasing in rate and intensity due to human activities (Brodie et al., 2021; Davies, 2019; Harfoot et al., 2021). For example, the greatest threats to tropical terrestrial vertebrates are logging and agriculture, and the threats posed by invasive species are particularly high for island birds (Harfoot et al., 2021). Species threatened with extinction are therefore distributed non-randomly across different regions, and their loss will lead to different rates of trait and phylogenetic diversity loss (Brodie et al., 2021). As a result, certain regions will be at increased risk from trait and phylogenetic homogenisation.

Here, we focus on birds as they exhibit a huge variety of phenotypes (Cooney et al., 2017; Hughes et al., 2022; Pigot et al., 2020; Tobias et al., 2022), are distributed across all terrestrial landmasses (Orme et al., 2005), and have high-quality trait and phylogenetic data available for most species (Cooney et al., 2017; Hughes et al., 2022; Jetz et al., 2012; Tobias et al., 2022; Wilman et al., 2014). We use a suite of morphological avian traits (beak size and shape, tarsus and wing length, and body size) that are likely to be linked to ecological function and so capture a species ecological niche (Pigot et al. 2016). Therefore, as species are lost, any decoupling of morphological and phylogenetic diversity may be relevant to ecological changes. Specifically, we assess whether the extinction of sequentially more inclusive IUCN extinction risk categories is expected to lead to morphological and/or phylogenetic homogenisation of the entire avian class and within each biome and ecoregion assemblage. Specifically, we investigate: (1) if species at greater risk of extinction have more unique traits; (2) the projected global loss of morphological and phylogenetic diversity; and (3) which ecoregions and biomes are most at risk of losing disproportionate amounts of morphological and phylogenetic diversity when compared to random species loss.

3.3 Methods

All data compilation, analysis and visualization were conducted in RStudio version 1.4.1717 (RStudio Team, 2021) and R version 4.1.1 (R Core Team, 2021). We follow the taxonomy used in the Jetz *et al*. (2012) phylogeny (see http://birdtree.org/).

3.3.1 Data collection

3.3.1.1 Morphological trait space

We compiled a raw dataset of ecologically relevant morphological traits following methodology outlined in Hughes *et al*. (2022) for 8455 of 9993 bird species. Our selected traits include the main seven principal components of beak shape (accounting for 98.9% of the total variation in beak shape) and bill size (centroid size) derived from 3D scans of museum specimens (Chira et al., 2018; Cooney et al., 2017; Hughes et al., 2022), and tarsus length (mm) and wing length (mm) taken from the corresponding museum specimens (Hughes et al., 2022). In addition, body size (g) was taken from the EltonTraits database (Wilman et al., 2014). These types of morphological traits have been closely linked to avian dietary and foraging ecology (Pigot et al., 2020, 2016). Bill size, wing length, tarsus length and body size were log10-transformed, and all trait data were then centred and re-scaled by standardising each to a mean of zero and unit variance (z-transformation). Finally, a principal components analysis (PCA) was run on the traits, and we selected the first eight PC axes (96.1% of total variation) from the resultant morphospace for analysis.

3.3.1.2 Threat status

We used data from the IUCN Red List (https://www.iucnredlist.org) (retrieved February 2020), to obtain threat statuses for each species with complete trait data (n = 8489), following the BirdTree taxonomy used in our dataset. Species categorised as Data Deficient (DD) (n = 20), Extinct in the Wild (EW)/ Extinct (EX) (n = 4) or Critically Endangered (Possibly Extinct) (CR(PE)) (n = 9) were excluded from our dataset. Where a species under the BirdTree taxonomy was listed as multiple species in the IUCN Red List taxonomy, we assigned the mean categorisation value. The resultant dataset contained 8455 species, with 6731 categorised as

Least Concern (LC), 812 as Near Threatened (NT), 527 as Vulnerable (VU), 274 as Endangered (EN), and 111 as Critically Endangered (CE).

3.3.1.3 Species pools

We defined a global pool of 8455 extant species with complete trait and threat status data. To account for regional and local spatial scales, we also generated species pools for 14 biomes and 814 ecoregions (Olson et al., 2001), excluding "Lake" and "Rock and Ice" categorisations. To do this, we obtained global distribution maps for all extant and probably extant species in our dataset from BirdLife International (http://www.birdlife.org/datazone/home), and projected these, as well as a spatial layer of ecoregions, onto a 100 km x 100 km equal area grid under Behrman cylindrical equal-area projection. Next, we recorded the presence/ absence of each species, and the dominant ecoregion in each grid cell. As each ecoregion exists in only one biome, we further matched biome identity to each grid cell. All 8384 species across 820 ecoregions and 14 biomes were categorised in this way, and for each ecoregion and biome we extracted a species list. Forty-two species that were not categorised during this process as a result of very small distributions, were manually assigned to the correct biomes and ecoregions (**Appendix 2 Section S1**). Due to the dimensionality of the trait data, at least nine species are needed for trait space calculations and thus six ecoregions with fewer than nine species were removed from our dataset. Three species were found exclusively in one of the removed ecoregions, and these were also dropped from our ecoregion species pools (**Appendix 2 Section S1**). Therefore, our final fourteen biome and 814 ecoregion species pools comprised 8426 and 8423 of 9993 (84.3%) species, respectively, with complete trait, conservation status, and range data present.

3.3.2 Phylogenetic signal across morphological traits

To assess the potential for decoupling of morphological diversity from phylogenetic history, we tested for multivariate phylogenetic signal across our morphological traits. We downloaded 200 complete species-level phylogenetic trees based on the Hackett backbone (Hackett et al., 2008) from http://birdtree.org/ (Jetz et al., 2012) and pruned each so that it only consisted of species in our dataset. We then used the transformPhylo.ML function in the R package MOTMOT (version 2.1.3: Puttick et al., 2020) to calculate the multivariate phylogenetic signal (Pagels λ (lambda): Pagel, 1999, 1997) of our eight PCs across every tree. A value of 1 shows high and a value of 0 shows no phylogenetic signal in traits.

3.3.3 Estimating the impact of threatened species loss on morphological and phylogenetic diversity

Our analyses were carried out at a global scale (across all 8455 bird species), regional scales (within biomes), and local scales (within ecoregions).

3.3.3.1 Morphological diversity loss

For each species pool, we first calculated the mean distance to centroid (i.e., the mean Euclidean distance from the morphospace centroid, also known as Functional Dispersion: Laliberté and Legendre, 2010), as a measure of morphospace size using the *dispaRity* R package (version 1.6.0: Guillerme, 2018). Next, we sequentially dropped species from the most to least threatened IUCN category (CR > EN > VU > NT) and re-calculated the mean distance to centroid for the remaining species. Our focus was to examine changes in morphospace size as threatened species were lost from their respective pools. A reduction in morphospace size (i.e., a lower mean distance to centroid) is indicative of morphological

homogenisation as species with more unique trait combinations than average are lost. We note that increases in mean distance to centroid can occur where species are primarily lost from the centre of morphospace. In addition, species could be lost such that no change in mean distance to centroid occurs. We therefore stress that this should not be used as evidence that species loss in these areas is not of conservation concern. Identifying significant incidences of morphological diversity loss is of crucial importance, alongside species loss, as the ecological consequences of morphological homogenisation are a particular conservation concern.

3.3.3.2 Phylogenetic diversity loss

To account for phylogenetic uncertainty, we calculated phylogenetic diversity (Faith, 1992) on all 200 phylogenetic trees (Jetz et al., 2012) for each species pool using the function *pd.query* in the R package *PhyloMeasures* (version 2.1: Tsirogiannis and Sandel, 2017). Phylogenetic diversity calculations were repeated for each species pool after sequentially dropping species from each IUCN category (CR, EN, VU, NT).

3.3.3.3 Null models

As morphological and phylogenetic diversity correlate with species richness (Safi et al. 2011; Voskamp et al. 2017; Hughes et al. 2022) (**Appendix 2 Figure S1**), we constructed null models to test whether the species remaining after losing each IUCN category had mean distance to centroid and phylogenetic diversity values that deviated from expected given the observed species richness. To do this, we sampled 1000 null assemblages for each value of species richness after losing CR, EN, VU, and finally NT species. For the global analysis, species sampled could be from the whole avian class; for each biome, species could be drawn from

that focal biome species pool; and for each ecoregion, species were sampled from that focal ecoregion pool. For each of the 1000 null assemblages, we calculated the mean distance to centroid, before calculating the mean and standard deviation of these 1000 values. Next, we calculated the standard effect size (SES) for each global, biome, and ecoregion community, by taking the null mean distance to centroid from the observed mean distance to centroid and dividing by the standard deviation of the null values:

$$SES = \frac{observed\ -\ mean(null)}{sd(null)}$$

We followed the same protocol to calculate the SES for phylogenetic diversity. SES scores were calculated for each of the 200 phylogenetic trees (Jetz et al., 2012) and we took the average SES score for each global, biome, and ecoregion community after losing each IUCN threat category. A positive SES value indicates a higher mean distance to centroid or phylogenetic diversity value than expected, whereas a negative SES indicates a lower value. Exceptional values of mean distance to centroid and phylogenetic diversity were those that showed statistically significant deviation from expected (+/- 2), with exceptionally negative values (< -2) indicating morphological or phylogenetic homogenisation of communities above that expected from species loss alone.

3.4 Results

3.4.1 Extinction risk across morphospace

Avian morphospace is distributed around a dense core of species in the centre, with fewer, more diverse forms found towards the edges of morphospace (**Figure 3.1**) (Chira et al., 2018; Hughes et al., 2022; Pigot et al., 2020). Size metrics predominantly load onto principal

component (PC) 1, capturing 35% variation in avian traits from the largest species (e.g., cranes [Gruidae]) to the smallest (e.g., hummingbirds [Trochilidae]). In contrast to the overall distribution of species, highly threatened (Critically Endangered (CR) and Endangered (EN)) species tend to be more evenly spread out across PCs 1 and 2 (**Figure 3.1**). Overall, however, we do not find a clear pattern of more highly threatened species occupying the edges of morphospace. When calculating distance to centroid for each species in our dataset, we find that as threat status decreases (i.e., species become less threatened), there is a weak trend of species tending to be closer to the centre of morphospace (**Appendix 2 Figure S2**). We treat this result with caution as there are wide errors around the mean values at each threat level.

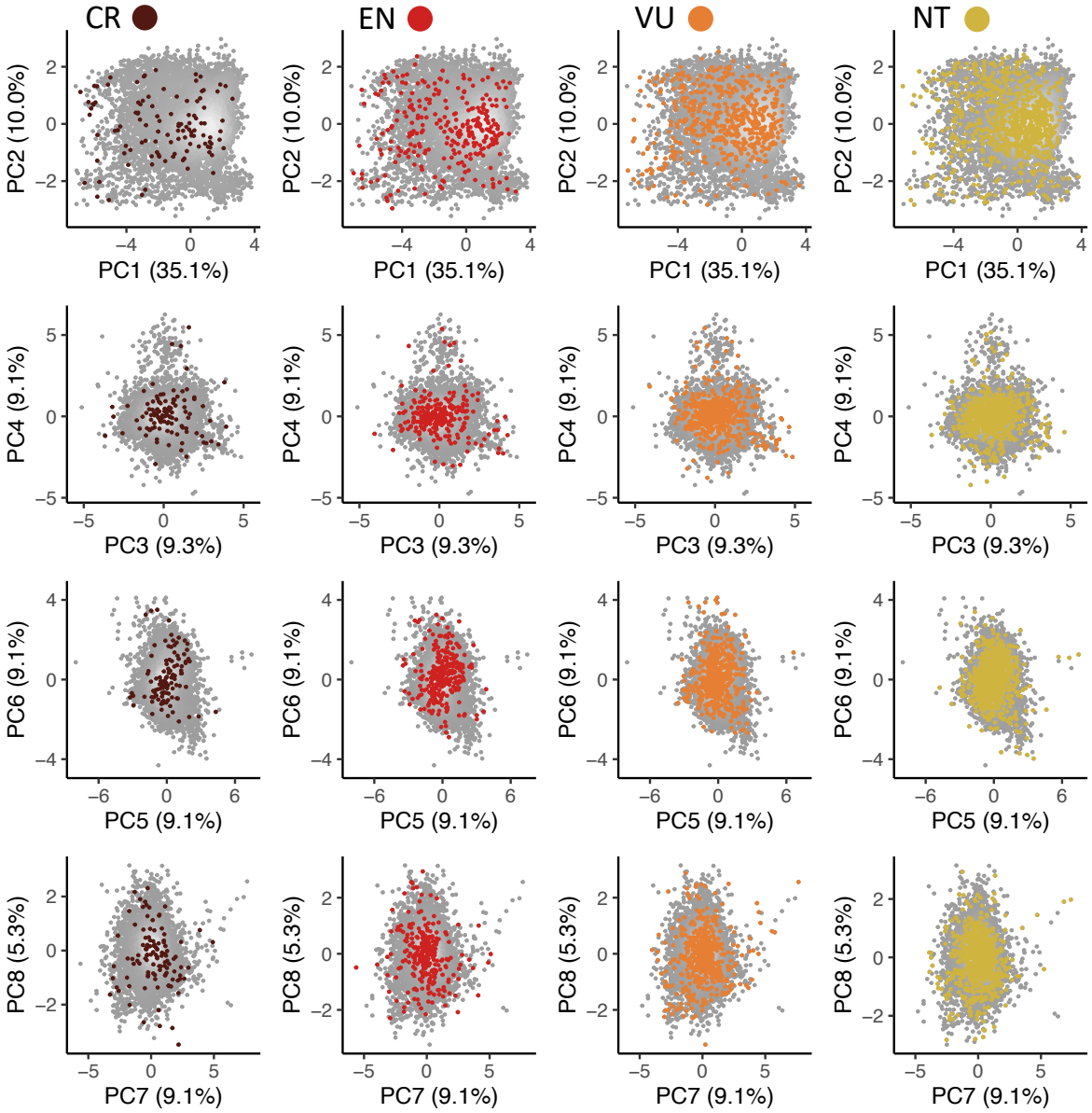

Figure 3.1: Scatterplots showing the first eight principal components of morphological traits, and the proportion of variation represented by each. Species classified in the IUCN red list as Critically Endangered (CR), Endangered (EN), Vulnerable (VU), and Near Threatened (NT) are coloured dark red through to yellow, whilst all other species are grey. Light grey shows where species density is highest.

3.4.2 Phylogenetic signal across morphological traits

We find a strong multivariate phylogenetic signal across our 8 principal components. However, there is evidence of departure from strict Brownian motion with a mean $\lambda = 0.920$ (lower confidence interval = 0.918, upper confidence interval = 0.923) across 200 phylogenetic trees.

3.4.3 Global loss of morphological and phylogenetic diversity

We find strong evidence of morphological homogenisation across the avian class (**Figure 3.2**). A standard effect size (SES) lower than -2 indicates a significantly greater loss of morphological deviation than that expected from species extinction alone. Losing 111 CR species leads to significant homogenisation of avian morphospace with a SES mean distance to centroid score of -7.89 (**Figure 3.2**). Morphological homogenisation continues with the additional loss of EN (SES = -12.00) and Vulnerable (VU: SES = -15.94) species, with no further reduction in mean distance to centroid SES with the loss of Near Threatened (NT: SES = -15.80) species (Figure 2), implying that NT species are lost at random across morphospace, unlike species threatened with extinction (CR, EN, VU).

We find that the loss of CR, EN, and VU species does not lead to a significant loss of phylogenetic diversity, above that expected through species loss alone (SES > -2: **Figure 3.2**). Only the additional loss of NT species results in a significant reduction in phylogenetic diversity (SES = -3.39: **Figure 3.2**), indicating that NT species are more evolutionarily distinct compared to the global pool of species.

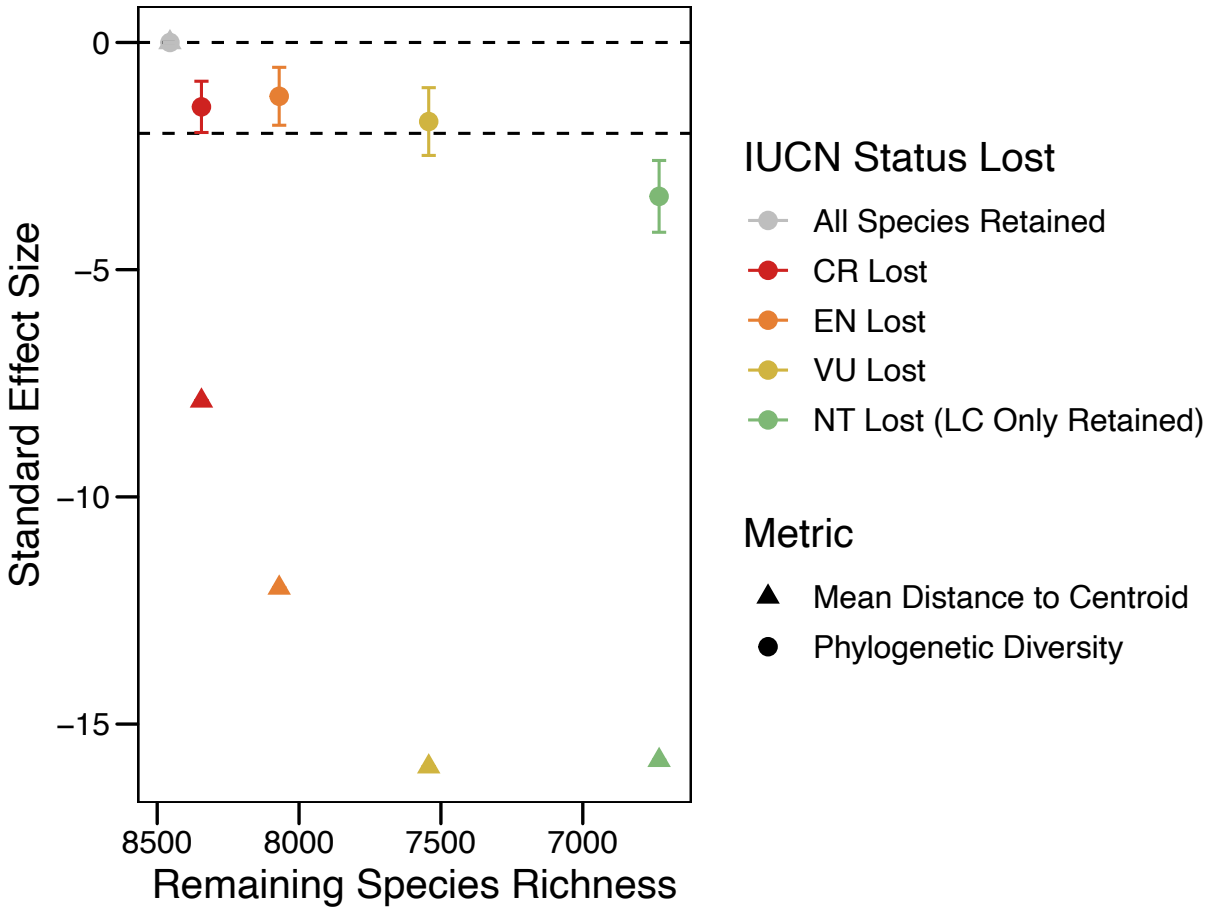

Figure 3.2: The standard effect size of mean distance to centroid (triangles) and phylogenetic diversity (circles), calculated for the whole global species pool of birds (grey, n = 8455), and for each remaining value of species richness where species categorised under each IUCN threat status are lost: critically endangered (CR: red) species, then endangered (EN: orange) species, vulnerable (VU: yellow) species, and finally near threatened (NT: green) species, leaving least concern (LC) species only. Error bars show the standard deviation of phylogenetic diversity calculated on 200 phylogenetic trees.

3.4.4 Spatial loss of morphological and phylogenetic diversity

3.4.4.1 Biomes

We find strong latitudinal variation in morphological diversity and phylogenetic diversity, with communities in the tropics harbouring the highest phylogenetic diversity and being particularly clustered around the centroid of morphospace (**Figure 3A, B**). If CR species went extinct, 12 of the 14 biomes (86%) would experience morphological homogenisation (SES < -

2) (**Figure 4A, Appendix 2 Table S1**), with the most imperilled biomes being tropical dry and moist forests, and flooded grasslands (**Figure 3C, Appendix 2 Table S1**). Morphological diversity loss is as expected given species richness loss in Mediterranean forest and temperate grassland (**Figure 4A, Appendix 2 Table S1**). All biomes would experience homogenisation with the further loss of EN, VU, and NT species (**Figure 3E, 4B, Appendix 2 Figure S3, S4**), with montane grassland becoming especially highly threatened with the loss of EN species (**Figure 3E, Appendix 2 Table S1**).

Phylogenetic diversity loss does not show significant homogenisation for most biomes when CR species are lost (13/14), with only Mediterranean forests experiencing exceptional homogenisation (**Figure 3D, 4A**). Likewise, when EN species are additionally lost, only the temperate broadleaf forest biome is threatened with phylogenetic homogenisation (**Figure 3F, 4B**). For both biomes, homogenisation is only just significant.

The loss of phylogenetic diversity does not correlate with a loss of morphological diversity when CR species only are lost (Pearson's product-moment correlation, $\rho = -0.397$, $p = 0.160$) and when EN species additionally are lost ($\rho = 0.417$ $p = 0.138$) (**Figure 4A, B**). As greater species richness is lost, the two are more closely correlated, with VU ($\rho = 0.787$, $p < 0.001$) and NT species loss ($\rho = 0.863$, $p < 0.0001$) showing an increasingly strong correlation (**Appendix 2 Figure S4**). Increasing numbers of biomes become threatened with homogenisation of phylogenetic diversity as VU (21%) and NT (50%) species are lost (**Appendix 2 Figure S3B, D**).

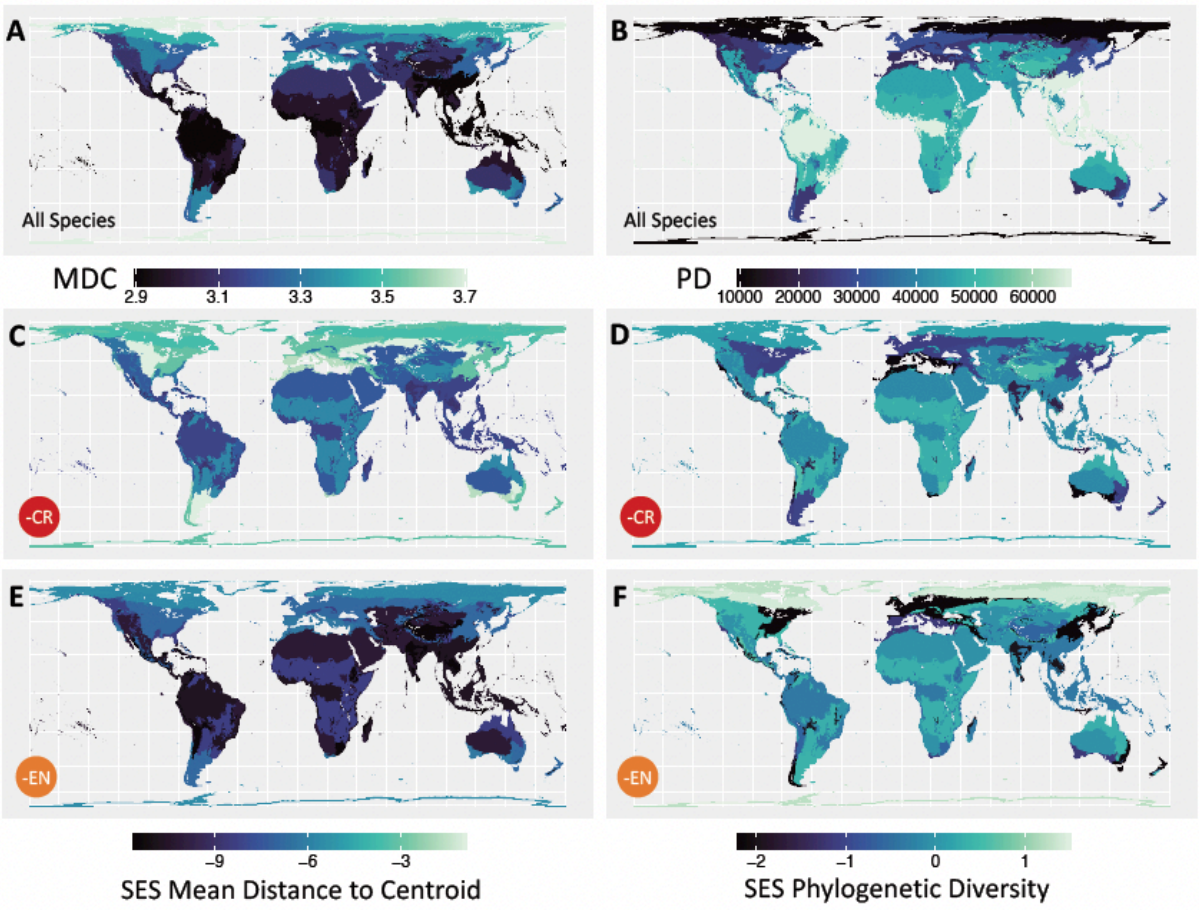

Figure 3.3: A) morphological diversity (mean distance to centroid) and B) phylogenetic diversity for 8426 bird species across 14 terrestrial biomes. Standard effect sizes (SES) for C) morphological and D) phylogenetic diversity were calculated after critically endangered (CR) species, and (E, F) additionally, when endangered (EN) species are dropped.

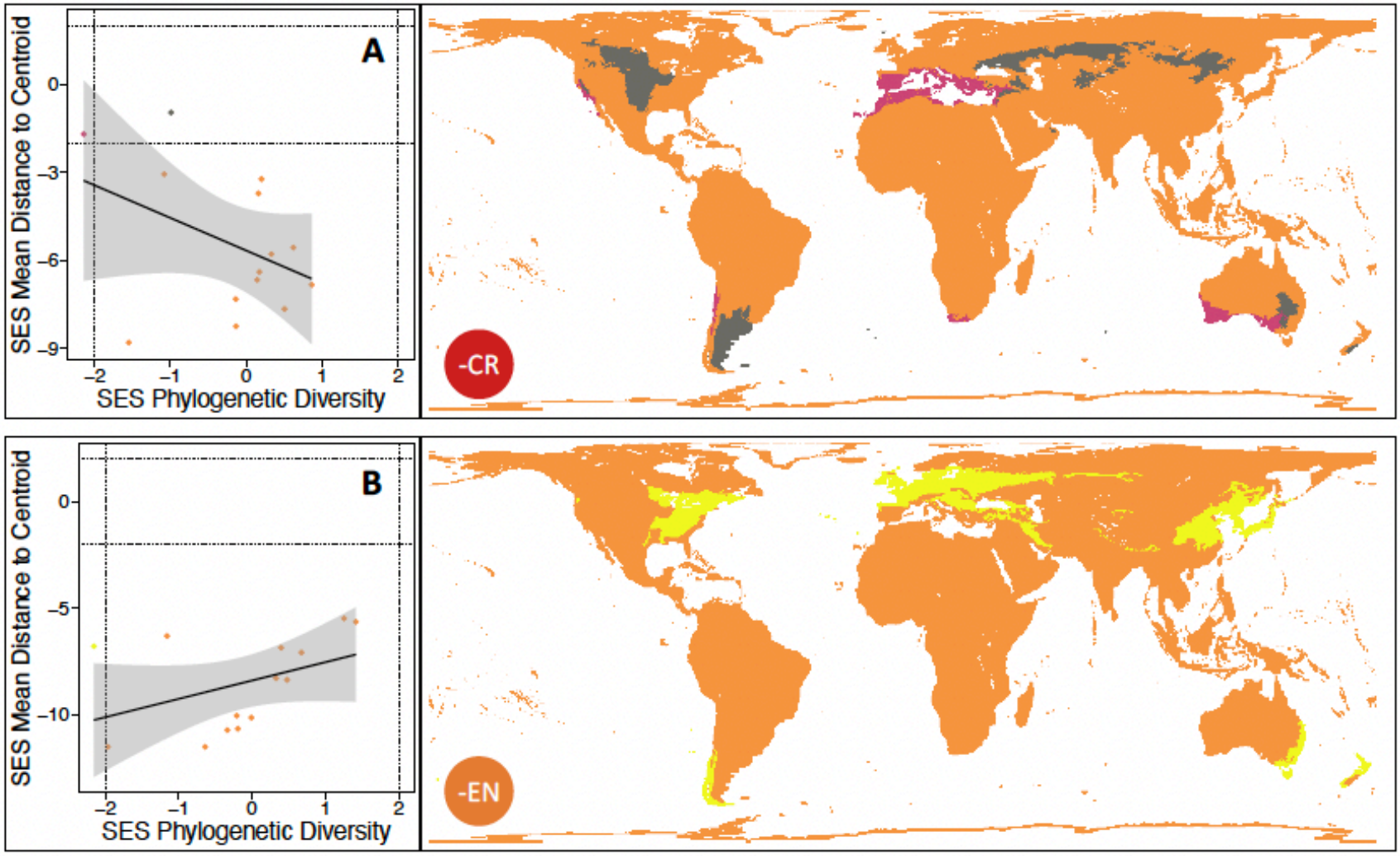
A
SES Mean Distance to Centroid
0
−3
−6
−9
−2
−1
0
1
2
SES Phylogenetic Diversity
-CR
B
SES Mean Distance to Centroid
0
−5
−10
−2
−1
0
1
2
SES Phylogenetic Diversity
-EN

Figure 3.4: Standard effect sizes (SES) of morphological diversity (mean distance to centroid) and phylogenetic diversity calculated for species assemblages in each global terrestrial biome (n = 14) where significant deviation from expected (+/- 2) is present. Homogenisation is indicated where SES is more negative than -2. Panel A shows significant SES scores calculated where assemblages are missing critically endangered (CR) species, and panel B shows this were endangered (EN) species are also missing. Dark grey indicates no significant deviation from expected.

3.4.4.2 Ecoregions

Overall, we find that species are particularly clustered around the centroid (i.e., low morphological diversity) in many East Asian ecoregions. The highest morphological diversity is found across ecoregions in New Zealand and the Southern tip of South America, as well as Northern North America (**Figure 5A**). Many ecoregions of the world would experience morphological homogenisation (mean distance to centroid SES < -2) if species in each IUCN category were to go extinct (**Figure 5C, E, Appendix 2 S5A, C**). For example, 48.4% of ecoregions would experience morphological homogenisation where CR species are lost (n = 382 ecoregions) (**Figure 6A**), and 53.3% where both CR and EN species are lost (n = 698 ecoregions) (**Figure 6B**). Ecoregions that are particularly morphologically imperilled are those found in the Himalayas and parts of Indochina (**Figure 5C, E**), with the addition of ecoregions across sub-Saharan and East Africa where VU and NT species morphology is lost (**Appendix 2 Figure S5A, C**).

Fewer ecoregions would experience phylogenetic homogenisation (SES < - 2) where CR (5.5% ecoregions, n = 382) and CR + EN species (4.3% ecoregions, n = 698) are lost (**Figure 6A, B**). The most phylogenetically imperilled ecoregions are found in parts of Indochina, particularly

Cambodia and Vietnam, as well as French Polynesia, Iberian and Pyrenean montane forests, and Australia (**Figure 5D, F, Appendix 2 Table S2**). Further loss of VU and NT species leads to the addition of central African ecoregions being threatened with phylogenetic homogenisation, as well as those covering the length of the Andes and Sulawesi (**Appendix 2 Figure S5B, D**).

We find that the loss of phylogenetic diversity correlates, albeit weakly, with the loss of morphological diversity (**Figure 6A**) when CR (Pearson's product-moment correlation, ρ = 0.160, $p < 0.01$) and CR + EN species are lost ($\rho = 0.181$, $p < 0.0001$) (**Figure 6B**). The correlation is stronger as VU ($\rho = 0.330$, $p < 0.0001$) (**Appendix 2 Figure S6A**), and NT ($\rho = 0.470$, $p < 0.0001$) species are further lost (**Appendix 2 Figure S6B**).

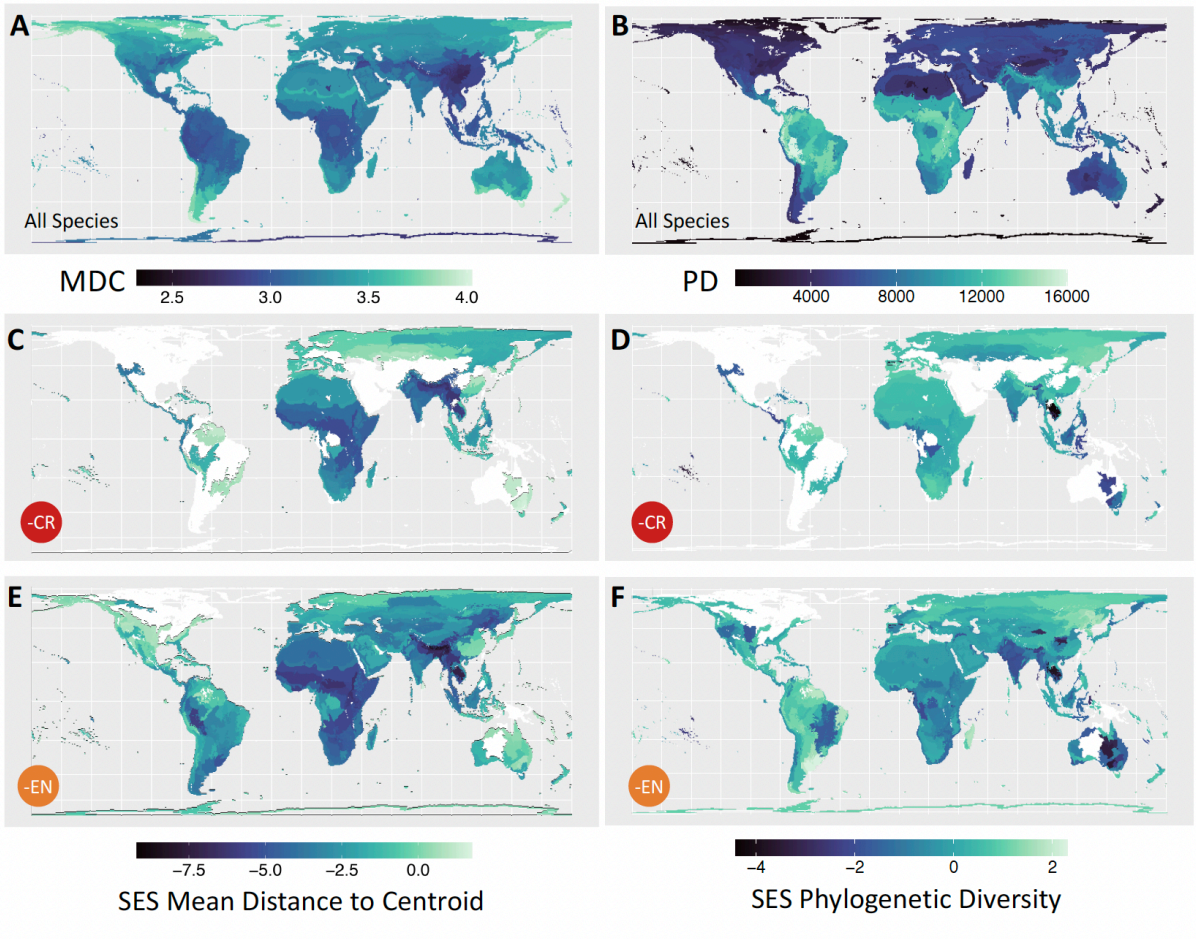

Figure 3.5: A) morphological diversity (mean distance to centroid) and B) phylogenetic diversity for 8423 bird species across 814 terrestrial ecoregions. Standard effect sizes (SES) for C) morphological and D) phylogenetic diversity were calculated after critically endangered (CR) species, and (E, F) additionally, when endangered (EN) species are dropped.

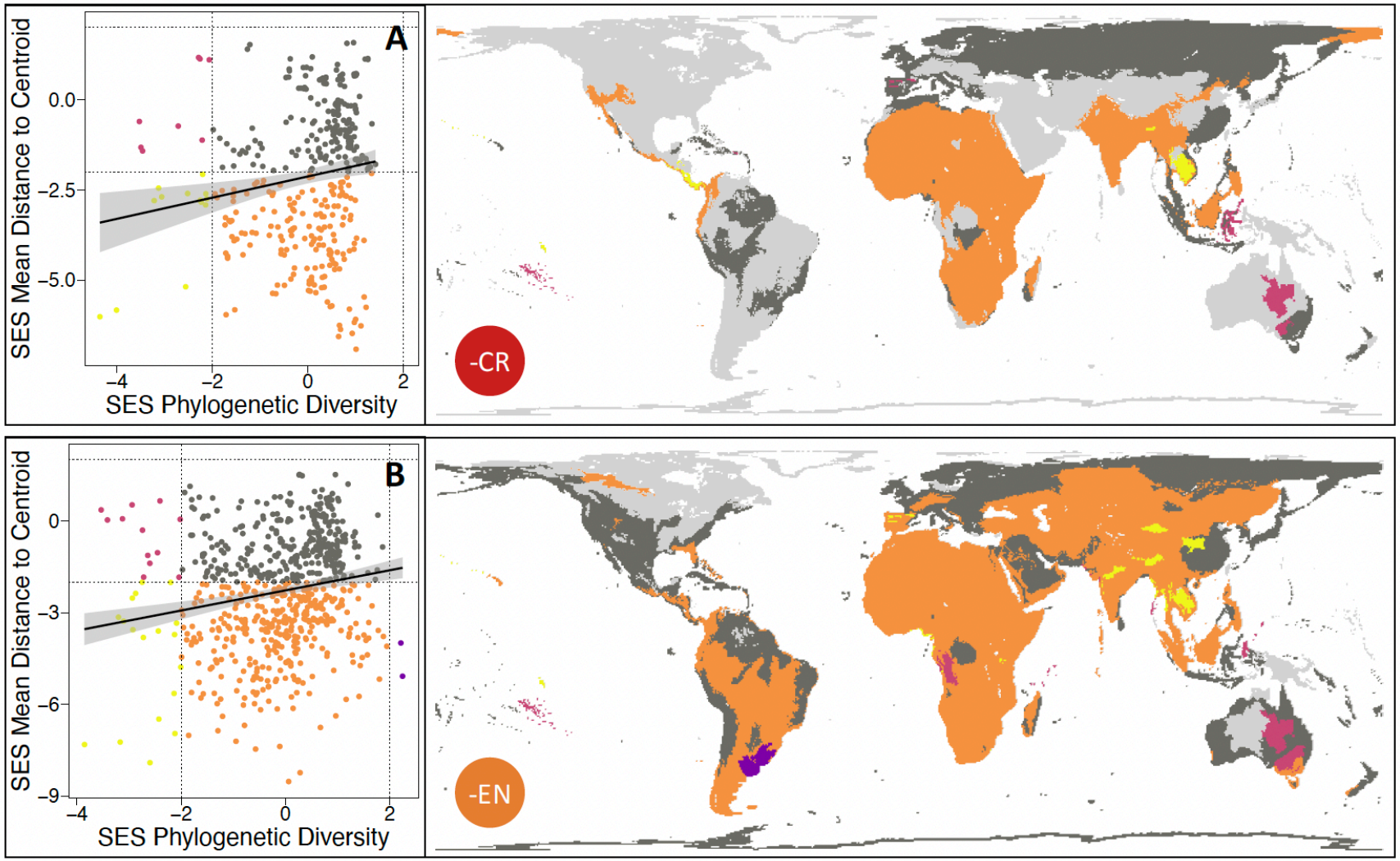
A
SES Mean Distance to Centroid
0.0
−2.5
−5.0
−4
−2
0
2
SES Phylogenetic Diversity
-CR
B
SES Mean Distance to Centroid
0
−3
−6
−9
−4
−2
0
2
SES Phylogenetic Diversity
-EN

Figure 3.6: Standard effect sizes (SES) of morphological diversity (mean distance to centroid) and phylogenetic diversity of species assemblages in each global terrestrial ecoregion (n = 814) where significant deviation from expected (+/- 2) is present. Homogenisation is indicated where SES is more negative than -2. Panel A shows significant SES scores calculated where assemblages are missing critically endangered species (CR), and panel B shows this were endangered (EN) species are also missing. Dark grey indicates no significant deviation from expected. Light grey indicates ecoregions with no CR or EN species.

3.5 Discussion

As the rate of extinction increases, understanding the impact of species loss on the ecological and evolutionary components of biodiversity has never been more important (Dirzo et al., 2014; Oliveira et al., 2020; Vane-Wright et al., 1991). Here, using a comprehensive set of ecologically relevant morphological traits, we find strong evidence for morphological homogenisation across the entire avian class, and across terrestrial biome and ecoregion assemblages. Bird species will become more similar to each other in terms of their morphology as species in each IUCN threat category are lost, and presumably this has already occurred where highly threatened species have been locally extirpated. Despite extant avian morphological and phylogenetic diversity correlating strongly, and strong phylogenetic signal in the traits we used, we do not find corresponding levels of phylogenetic homogenisation. Whilst phylogenetic diversity loss is a robust proxy for capturing feature diversity loss (Faith, 2008, 1992), our results highlight that phylogenetic diversity loss is not always an appropriate surrogate for morphological diversity loss (Kelly et al., 2014; Mazel et al., 2018; Oliveira et al., 2020), at least in birds and for this set of traits.

Our findings of a lack of congruence between morphological and phylogenetic diversity loss across the avian class indicates that species threatened with extinction exhibit traits that are more unique, given their phylogenetic history, compared to the wider species pool. Deviations from Brownian motion are prevalent for the morphological traits we used, with extensive variation in their evolutionary rates across the phylogenetic tree (Chira et al., 2018; Cooney et al., 2017). Consequently, some lineages on relatively short branches have diverged rapidly, decoupling the relationship between phylogenetic and morphological uniqueness. At a global scale, morphological homogenisation increases as critically endangered (CR) species, and subsequently endangered (EN) and vulnerable (VU) species are lost, with remaining species becoming increasingly alike in terms of their morphology, meaning certain morphologies are lost. The main axis of morphological variation in birds is size, and size is subsequently dominant on principal component (PC) 1 of avian morphospace (Cooney et al., 2017; Hughes et al., 2022; Pigot et al., 2020 etc.). Cooke *et al.* (2019) found an "ecological downsizing" effect on birds and mammals whereby predicted species extinctions drove the loss of larger species, resulting in surviving species being smaller. Whilst we do not find a clear pattern of more imperilled species occupying the edges of avian morphospace (Cooke et al., 2019), we find some indication that CR species are found less frequently than expected at smaller sizes (PC1). Importantly, our results support the prediction that morphological diversity will decrease at a greater rate than expected through species loss alone in the face of global change (Oliveira et al., 2020).

At smaller spatial scales, morphological homogenisation could lead to a considerable loss of ecological roles and ecosystem functioning, productivity, and services (Clavel et al., 2011). Overall, we find that morphological but not phylogenetic homogenisation is an inevitable

outcome of predicted biodiversity loss for the majority of biomes and ecoregions. Of six critically endangered species lost in the top five most imperilled ecoregions, four of these are vultures (*Sarcogyps calvus, Gyps tenuirostris, Gyps bengalensis*, *and Gyps indicus*). The traits used in this study are broadly similar to those linked to the ecological foraging guilds of birds (Pigot et al., 2020, 2016), and vultures as large-bodied, obligate scavengers, fill distinct areas of morphospace (Bright et al., 2016; Hughes et al., 2022). Therefore, it is likely that the considerable loss of morphological diversity in the Himalayan ecoregions is partly driven by the loss of vultures – the most imperilled group of birds (Buechley and Şekercioğlu, 2016). Vultures provide vital ecosystem services by removing decaying carcasses, which would otherwise increase the direct transmission of infectious diseases (DeVault et al., 2016; Moleón et al., 2014; Ogada et al., 2012) and increase populations of opportunistic scavengers (i.e., dogs and rats) that spread rabies and bubonic plague (DeVault et al., 2016; Markandya et al., 2008).

Another region containing assemblages at risk of morphological homogenisation are the dry and moist forest ecoregions of South Vietnam and Cambodia, where there is also exceptionally high expected loss of phylogenetic diversity. The CR and EN species here are therefore likely to be phylogenetically unique and exhibit sets of traits that the surviving species pool does not contain. Indeed, highly threatened species here are amongst the highest EDGE classified species – i.e., evolutionarily distinct and globally endangered (Jetz et al., 2014) (https://edgeofexistence.org/birds/) –including giant ibis (*Thaumatibis gigantea*, ranked 2nd by EDGE), Bengal florican (*Houbaropsis bengalensis*, 7th), and white-shouldered ibis (*Pseudibis davisoni*, 16th). Despite phylogenetic diversity increasingly being stated as an essential facet of biodiversity to conserve to meet global targets of biodiversity conservation

(e.g., IPBES, 2019), these species are currently only receiving low, medium, and very low conservation attention, respectively (https://edgeofexistence.org/birds/).

Despite being less widespread than morphological diversity loss, phylogenetic diversity loss remains an important metric for assessing the impact of species extinction (Faith, 1992). Specific sets of traits are used to capture morphological diversity that are expected to relate to specific ecological niches and functions in the present day (Petchey and Gaston, 2006), but it is impossible to capture all possible combinations of traits that species represent to exactly map form to function (Faith, 1992). Phylogenetic diversity captures this feature diversity, including traits not currently known or measurable (Faith, 2008, 1992). In turn, this makes phylogenetic diversity a good indicator of biodiversity "option value" – the unknown future benefits to humans that are not currently realised (Faith, 1992). Using subsets of ecologically relevant traits allows us to measure the impacts of species loss on specific aspects of phenotype, which may be important to conserve if they link to key aspects of ecosystem functioning or services (Flynn et al., 2011). Priority should therefore be given to establishing whether measurable species traits can more directly capture important features to conserve than phylogeny.

Our study focuses on species extinctions as a primary driver of morphological and phylogenetic homogenisation (McKinney and Lockwood, 1999). While we capture the range expansion of species to present day, including reintroduced species ranges, we do not include species' presence in a biome or ecoregion where they have been introduced through direct/ indirect human activity. The introduction and spread of non-native species are another key driver of the biological extinction crisis (Blackburn et al., 2019), and can diminish the

distinctiveness of regional assemblages, reducing trait and phylogenetic differences between species (Daru et al., 2021; Socolar et al., 2016; Yang et al., 2021). Across many assemblages, introduced species do not fill the resultant gaps in trait diversity caused by the extinction of species with more unique morphologies (Sayol et al., 2021), since they tend to be more generalist (Clavel et al., 2011; McKinney and Lockwood, 1999). Furthermore, we deal with global extinction but not local extirpation. In many areas, species are already functionally extinct across most of their ranges, and so morphological diversity is already likely to be dramatically constrained (Anderson et al., 2011). Given that the replacement of more specialist species by a smaller number of more generalist species (Clavel et al., 2011; McKinney and Lockwood, 1999) is unlikely to abate, it is likely that our findings underestimate the degree of morphological homogenisation that will and has already occurred during the Anthropocene.

In conclusion, our work reveals widespread morphological homogenisation across the entire avian class, most terrestrial biomes, and half of all ecoregions. The loss of morphological diversity exceeds that predicted by threatened species loss alone, and highlights important losses of ecological function across assemblages, with important ramifications for humans as ecosystem services are lost. Phylogenetic diversity tends to decline as expected as species go extinct, with few assemblages threatened with phylogenetic homogenisation. Whether measurable species traits can capture features of conservation priority, such as key ecosystem services, more directly is crucial to understand when assessing the impacts of extinction on biodiversity.

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CHAPTER 4

The effects of tropical secondary forest regeneration on avian phylogenetic diversity.

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A PDF of the Journal of Applied Ecology manuscript is provided at the end of this Thesis in the Key Publication section.

4.1 Abstract

The conversion of tropical forests to farmland is a key driver of the current extinction crisis. With the present rate of deforestation unlikely to subside, secondary forests that regenerate on abandoned agricultural land may provide an option for safeguarding biodiversity. While species richness (SR) may recover as secondary forests get older, the extent to which phylogenetic diversity (PD)—the total amount of evolutionary history present in a community—is conserved is less clear. Maximising PD has been argued to be important to conserve both evolutionary heritage and ecosystem function. Here, we investigate the effects of secondary forest regeneration on PD in birds. The regeneration of secondary forests could lead to a community of closely related species, despite maintaining comparable SR to primary forests, and thus have diminished biodiversity value with reduced evolutionary heritage. We use a meta-dataset of paired primary and secondary forest sites to show that, over time, forest specialist species returned across all sites as secondary forest age increased. Forest specialists colonise secondary tropical forests in both the Old World and the New World, but recovery of PD and community composition with time is only evident in the Old World. Whilst preserving primary tropical forests remains a core conservation goal, our results emphasize the important role of secondary forest in maintaining tropical forest biodiversity. Biodiversity recovery differs between Old and New World secondary forests and with proximity to primary forest, highlighting the need to consider local or regional differences in landscape composition and species characteristics, especially resilience to forest degradation and dispersal capability. While farmland abandonment is increasing across marginal areas in the tropics, there remains a critical need to provide long-term management and protection from reconversion to maximize conservation benefits of secondary forests. Our study suggests such investments should be focused on land in close proximity to primary forests.

4.2 Introduction

The biggest driver of the current extinction crisis is the conversion of tropical forest to farmland (Laurance et al., 2014). Over 150 million hectares of tropical forest were converted to farmland between 1980 and 2012 (Gibbs et al., 2010; Hansen et al., 2013). However, in many areas, agricultural land has been abandoned resulting in the regeneration of secondary forests (Aide et al., 2013). These secondary forests could help to reduce biodiversity loss (Chazdon, 2014) by providing an alternative to primary forests for species that would otherwise go extinct (Wright and Muller-Landau, 2006). Species richness (SR) often recovers with secondary forest age (Acevedo-Charry and Aide, 2019; Barlow et al., 2007; Gilroy et al., 2014), and many forest specialists that are threatened by forest loss may also re-colonize secondary forests (Basham et al., 2016; Gilroy et al., 2014). However, our understanding of how biodiversity metrics other than SR differ between primary and secondary forests is limited.

One such gap in our knowledge is whether secondary forests conserve or support recovery of phylogenetic diversity (PD)—the total amount of evolutionary history present in a community (Faith, 1992). PD is potentially important for several reasons. First, while functional diversity—the range of functional roles occupied by species within a community (Petchey and Gaston, 2006)—and PD may not be perfectly correlated, prioritizing the conservation of PD is also expected to conserve functional diversity (Faith, 1992; Mazel et al., 2018, 2017; Pavoine et al., 2013). Functional redundancy increases as secondary forest age increases, potentially leading to greater resilience in ecosystem services (Sayer et al., 2017). Moreover, it has been argued that conservation objectives focused on a narrow set of functional traits could lead to the loss of PD. This is because there are many potential axes of functional diversity that are

typically condensed to a subset of traits that are easy to measure and/or widely available. Instead, PD may more effectively capture a wide suite of traits encapsulated under the concept of feature-diversity, defined broadly as the different evolutionary features of diversity (Faith, 1992; Owen et al., 2019). Second, phylogenetically diverse communities are more likely to hold evolutionarily distinct or relict species with few close relatives (Jetz et al., 2014) and so harbor a disproportionately large amount of evolutionary history. Third, there is intrinsic value in conserving as much of the world's evolutionary heritage as possible (Winter et al., 2013). Therefore, understanding how PD recovers and the mechanisms that drive this recovery is critical to understanding the conservation potential of secondary tropical forests.

Recovery of SR alone is unlikely to be an informative guide to the conservation value of secondary forests as SR (i.e., alpha diversity) tells us nothing about community composition. Conversion of forest to agriculture could result in the loss of forest-dependent or disturbance-sensitive species, and the gain of disturbance-tolerant species or species adapted to more open habitats. As such, whilst SR may recover rapidly following abandonment, it may markedly differ in community structure, phylogenetic composition, and ecosystem function. However, subsequent succession towards secondary forest may allow the return of forest-dependent species. Large frugivores and understory insectivores, for example, are particularly forest dependent and sensitive to disturbance (Powell et al., 2015; Şekercioğlu, 2012; Şekercioğlu et al., 2002) so may require time for secondary forest to mature before returning. In addition, species with low dispersal abilities may have a reduced ability to re-colonise secondary forests (Laurance and Gomez, 2005; Moore et al., 2008), particularly if secondary forest patches are far from the remaining primary forest source pool.

At one extreme, the same set of species originally found in the primary forest prior to conversion to agriculture could re-colonise the secondary forest resulting in the simultaneous recovery of SR, community composition, and PD. At the other extreme, community intactness may be substantially degraded. PD in intact primary forest tends to be greater than expected by chance and rapid land-use change results in phylogenetic clustering of communities as PD is lost rapidly with increasing agricultural intensification (Frishkoff et al., 2014; Prescott et al., 2016). This leads to the prediction that young secondary forests should have low PD compared to primary forests whereas differences in SR may be comparatively minor. If secondary forest provides a viable alternative habitat for primary forest species, then PD should increase with age as the forest matures (e.g., Edwards et al., 2017). The effect of variability in species traits and of the landscape matrix is that recovery of SR, community composition, and PD may be further mediated by the degree of isolation of secondary forest patches, with stalled or slow recovery in the most isolated secondary forests.

Here, we conduct the first pan-tropical assessment of change in PD with secondary forest age. We focus on birds, because they are functionally important components of ecosystems (Şekercioğlu et al., 2016). Specifically, we assess if SR and PD varies between primary and secondary forests and whether the secondary forest communities attain comparable SR and PD to paired primary forests communities as time since abandonment increases. We further assess how distance to primary forest, biogeography (Old World versus New World) and climate mediate variation in the recovery of tropical forest bird communities.

4.3 Materials and Methods

4.3.1 Data collation

A total of 20 pan-tropical studies containing 35 paired secondary and primary forest sites were selected from a review by Sayer et al. (2017) (**Appendix 3 Table S1**). Seven sites included by Sayer et al. (2017) were considered unsuitable for the present study (i.e., due to incomplete species lists, ambiguous secondary forest ages etc.) and were excluded (**Appendix 3 S1**). All sites included were in the tropics and sub-tropics with 21 in the New World and 14 in the Old World (**Figure 4.1**). Primary forest sites are native forests with no evidence of previous deforestation and degradation. Secondary forest sites are defined as areas undergoing succession after all or nearly all trees had been removed to make way for agriculture (Corlett, 1994). Forests recovering after fires or sites that had been selectively logged were not included in this definition.

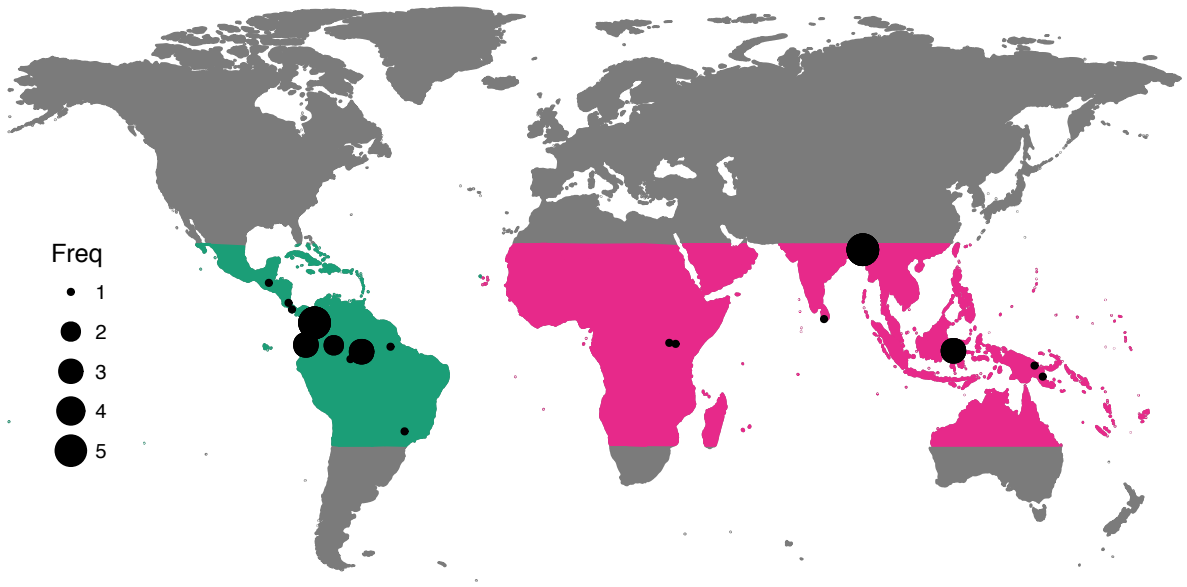

Figure 4.1: The distribution of the 35 paired sites in this study. Sites were chosen within 24 degrees of latitude from the equator. The number of paired sites per study area is indicated by circle size. The New World is coloured green and the Old World is coloured pink.

The ages of secondary forest sites were given in each study as single ages or age ranges where similarly aged stands were grouped together. In the latter instance, the median values of secondary forest patches were calculated (Sayer et al., 2017). Where available, we extracted the distances between paired primary and secondary forest sites from measured values, or qualitative descriptions given in the studies considered (n=31) (**Appendix 3 Table S1**). Each of the chosen studies sampled the entire local avian community in both primary and secondary forest patches using consistent methods within studies, but which varied between studies (i.e., point counts, mist netting, transects). Specific information regarding how each species observed used the habitat (e.g., foraging, breeding etc.) were not described.

We also collected data for three environmental variables at each site. Elevation (metres above sea level) for each site was obtained from the GTOP030 global digital elevation model (GTOPO30 DEM, 1996) using Google Earth Engine (Gorelick et al., 2017). Mean annual temperature and mean annual precipitation were extracted for each site from the WorldClim database (Fick and Hijmans, 2017). Elevation, precipitation, and temperature were log-transformed prior to analysis.

4.3.2 Measures of species richness and phylogenetic diversity

For each study site, we calculated the number of different species present in each community (SR, species richness), and beta diversity (*ßTD*, (Whittaker, 1972, 1960)), and phylogenetic beta diversity (*ßPD*, (Bryant et al., 2008; Graham and Fine, 2008)) as measures of community intactness, for each paired primary and secondary forest site. We calculated the Sørenson index in the R package vegan (version 1.4-2: Oksanen et al. (2008)) as a measure of *ßTD*, to assess the losses of species from each secondary forest site compared to the corresponding

paired primary site. *ßPD* was measured as a fraction of the phylogenetic branch-lengths present in secondary forest communities that were also present in paired primary forest communities using the *phylosor* function in the R package picante (version 1.6-2: Kembel et al. (2010)).

We also calculated three phylogenetic diversity metrics and their standardised effect sizes using the R package picante (version 1.6-2: Kembel et al. (2010)). These were: phylogenetic diversity (PD, the total amount of evolutionary history represented by a community (Faith, 1992); mean pairwise difference (MPD, average phylogenetic distance between every combination of paired individuals in a community, Webb et al. (2002)); and the mean nearest taxon distance (MNTD, average phylogenetic distance between an individual and its closest relative in the community, Webb et al. (2002)). Because PD, MPD, and MNTD can all scale with SR (Webb et al., 2002) we calculated standardised effect sizes for each raw phylogenetic diversity measure using the 'richness' algorithm in picante. This maintains SR for each site but allows the random selection of species from a wider species pool (Webb et al., 2002). We refer to these metrics as ses.PD, ses.MPD, and ses.MNTD, respectively. A full description of the metrics, including the equations used, are available in **Appendix 3 Table S2**.

Species pools were generated by downloading species lists from http://mol.org/ (Map of Life, 2017) for a 50 km radius around each study site. Map of Life uses species range maps (e.g., BirdLife International), as well as data from additional sources such as point count data from published studies. A 50 km radius was chosen for three reasons. Firstly, it allows the inclusion of all species that are likely to occur at each site. Secondly, previous studies have shown that finer spatial resolutions are not practical given the quality of range maps and can give an

inaccurate representation of observed species pools (Hurlbert and Jetz, 2007). Thirdly, the Map of Life database only allows for a radius of 50 km to be selected. Including all species within a 50 km radius of each site could result in species appearing that would never occur at our sites, particularly in areas that are topographically diverse or at the margins of distinct biomes. To investigate the impact of changing species pools, we ran analyses on subsets of our species pools (all species, and forest only species), and found similar results in both instances (**Appendix 3 Tables S5, S6**).

We downloaded 500 phylogenetic trees based on the Hackett backbone (Hackett et al., 2008) from http://birdtree.org/ (Jetz et al., 2012) and calculated all metrics on every tree to account for phylogenetic uncertainty. For each measure of phylogenetic diversity and for *ßPD*, the 500 values were found to be normally distributed and an arithmetic mean value was taken for each site or paired site community.

4.3.3 Statistical analysis

We used linear mixed-effects models in the lme4 R package (version 1.1-13: Bates et al. (2014)) with RStudio version 1.0.136 (RStudio Team, 2016) and R version 3.3.2 (R Core Team, 2016). We included study identity as a random effect in all models because study areas included multiple secondary forest sites with a single primary forest site (**Appendix 3 Table S1**). As differing evolutionary histories and biogeographic variation in dispersal may influence phylogenetic diversity recovery patterns, we compared New World and Old World sites. For each analysis, models were constructed with either the fixed effect of forest type (primary or secondary), or secondary forest age and distance between primary and secondary sites, as well as the random effect of study identity. Secondary forest age and distance between

primary and secondary sites were log-transformed. These models were compared to a null intercept only model, with study identity as a random intercept. Residuals for each model were checked for normality and homoscedasticity. Likelihood ratio tests (LRTs) were used to compare models. We added our three climatic predictors in turn to the best fitting age and distance models for each response variable and region combination.

4.3.3.1 Primary versus secondary forests

We analysed the effect of forest type on SR and each of the raw phylogenetic diversity metrics.

4.3.3.2 Species and phylogenetic community composition

We tested the effect of secondary forest age, and distance between paired primary and secondary forest sites, on community intactness. We calculated community intactness for *ßTD* and *ßPD* between paired primary and secondary forest sites using a restricted species pool containing just primary forest species (n=1179).

4.3.3.3 Species and phylogenetic diversity

We next examined changes in phylogenetic diversity with time since secondary forest abandonment. We calculated our metrics on all species (n=1519), and also on a reduced subset, excluding species that were defined by BirdLife International as "Non-forest" (does not normally occur in forested habitat). The remaining 1478 species were categorised as having either "High" (forest specialists, always, or nearly always recorded in primary forest), "Medium" (largely found in primary forest, but often occurs, and can breed, in degraded habitat) or "Low" (can occur in primary forest, but more often found, and breeds, in degraded

habitat) forest dependency (Birdlife International, 2017; Buchanan et al., 2008) (Figure S1). When considering only forest species in our analyses, we likewise reduced the species pools used for calculating standardised effect sizes by removing species that were defined as not dependent on forests (Birdlife International, 2017).

We calculated the log response ratio (Hedges et al., 1999) as the log proportional difference between the means of each metric (SR, PD, MPD, MNTD) in secondary forest sites and primary forest sites. Values of ses.PD, ses.MPD and ses.MNTD can be negative, and so raw differences between paired secondary and primary forest were calculated.

4.3.3.4 Forest dependent species

We investigated whether the proportion of forest dependent species at each site became more equal as secondary forest age increased. For each site, we calculated the percentage of the avian community that were classed by Birdlife International (2017) as having "High" forest dependency, before calculating the difference between those percentages for each paired secondary and primary forest sites.

4.4 Results

Across all study sites, 1519 unique species were recorded spanning 87 avian clades (**Figure 4.3**). We found large clades in Old World sites with similar numbers of species found in both primary and secondary forest types (i.e., Shrikes and Monarchs, Pigeons and Doves, Cuckoos), with the exception of the Chats and Old World Flycatchers with higher SR in secondary forest sites. Some families with only a single species represented across all study sites were present in primary but not secondary forests (e.g., Whipbirds and Allies: *Ptilorrhoa caerulescens*,

Bowerbirds: *Ailuroedus buccoides*). In the New World, many avian clades were species rich in both primary and secondary forests (e.g., Woodpeckers, Trogons (**Figure 4.2**), Manakins and Cotingas) (**Figure 4.3C**). Some very small clades were present in only primary (Potoos and Sunbittern) or only secondary forest sites (e.g., Sparrows and Dippers). Several young passerine clades (e.g., Tanagers, Grosbeaks, Cardinals, Buntings, New World Blackbirds, New World Warblers) were more species rich in secondary than primary forests.

Figure 4.2: Slaty-tailed Trogon (*Trogon massena*) Female. 28th March 2022, Parque Nacional Volcán Arenal.

4.4.1 Primary versus secondary forests

Primary forests had a similar SR to secondary forests across the tropics (LRT: χ^2=1.01, p=0.315), in the New World (likelihood ratio test: χ^2=0.26, p=0.609), and in the Old World (LRT: χ^2=1.43, p=0.232). PD did not differ between primary forests and secondary forests across all sites (LRT: χ^2=2.45, p=0.118), Old World sites (LRT: χ^2=2.63, p=0.105), or New World sites (LRT: χ^2=0.52, p=0.469). Similarly, we found no differences in ses.PD, MPD, ses.MPD, MNTD or ses.MNTD between primary and secondary forests, in the New World, Old World, and across all sites (**Appendix 3 Table S3**).

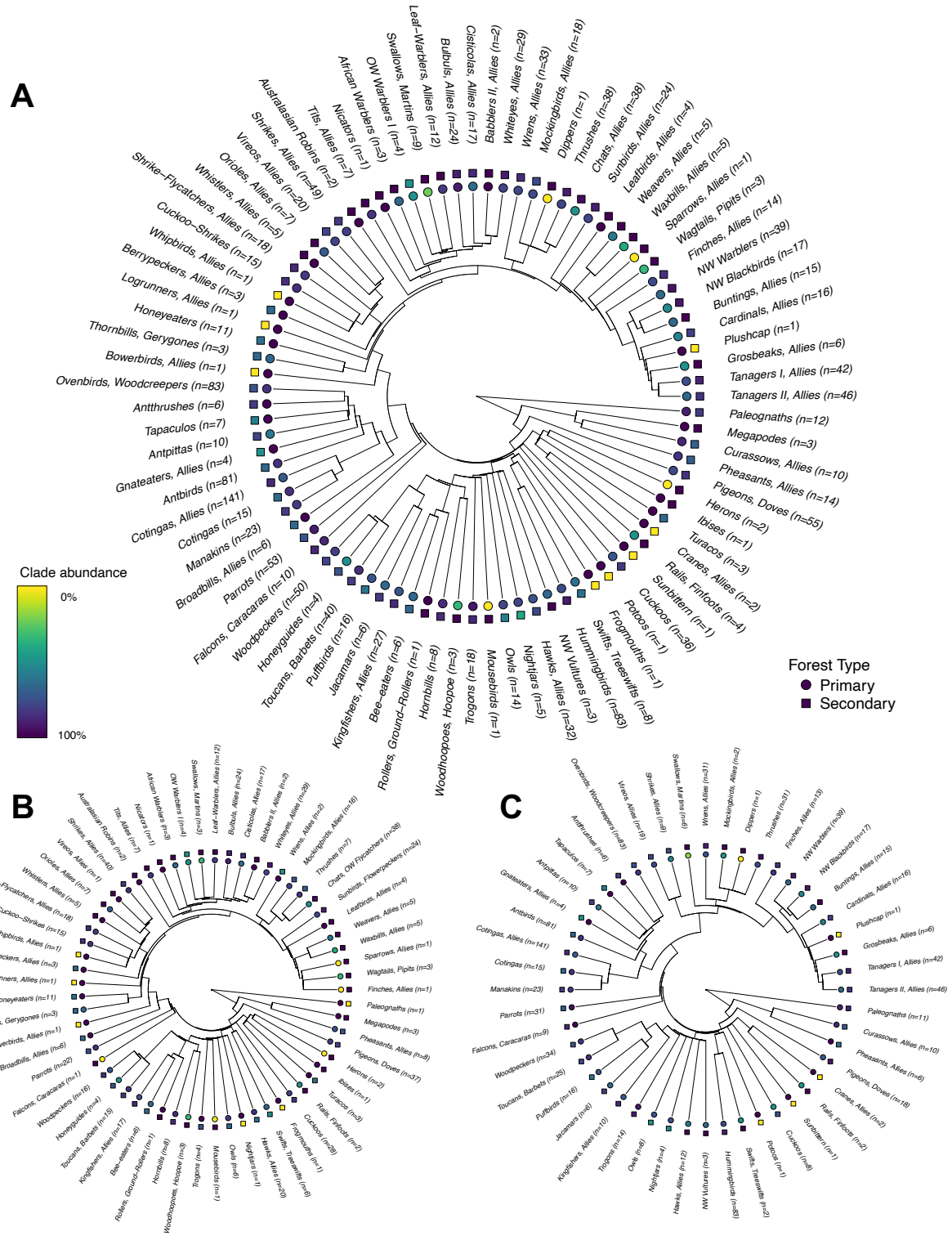

Figure 4.3: Phylogenetic distribution of avian clades in secondary and primary forests across **A)** all study sites, **B)** Old World sites, and **C)** New World sites. Spots and squares show a clades presence in primary and secondary forest respectively. The colour scale bar shows the proportion of species in a clade which is found in that particular habitat type.

4.4.2 Species and phylogenetic community composition

Avian communities in paired secondary and primary forest sites in the Old World became increasingly similar in both species (*ßTD*; **Figure 4.4A, Appendix 3 Table S4**; LRT: χ^2=17.71, p<0.001) and phylogenetic (*ßPD*; Figure 3B, Table S4; LRT: χ^2=19.51, p<0.001) composition with increasing time since abandonment. Based on estimated slopes, secondary forest species and phylogenetic composition would equal that of primary forests after 97-years and 92-years, respectively. In the Old World, distance between secondary and primary forest sites did not influence phylogenetic (LRT: χ^2=0.16, p=0.685), or species community intactness (LRT: χ^2=0.19, p=0.665) (**Figures 4.4C, D, Appendix 3 Table S4**). We also found a significant interaction with distance for both *ßTD* and *ßPD* where recovery appeared to be more rapid in more isolated sites (**Appendix 3 Table S4**). We suggest that the counterintuitive result may be spurious because only three Old World sites are isolated from primary forest and in those sites distance and age have a perfect rank correlation.

We found no change in *ßTD* (LRT: χ^2=0.01, p=0.923) or *ßPD* (LRT: χ^2=0.05, p=0.827) between paired primary and secondary forest communities in the New World as time since disturbance increases (**Figures 4.4A, B, Appendix 3 Table S4**). Indeed, soon after land abandonment, New World communities retained around 72% of species and 79% of phylogenetic intactness compared to primary forest communities, and this did not significantly change across the 50-year study period. However, we found that as distance between sites increases, the number of primary forest species that are found in New World secondary forest sites decreases (LRT: χ^2=5.43, p=0.020), but that phylogenetic intactness (LRT: χ^2=3.30, p=0.069) did not change (**Figures 4.4C, D, Appendix 3 Table S4**). We found no effect of any of the climatic predictors on species or phylogenetic community intactness (**Appendix 3 Table S8**).

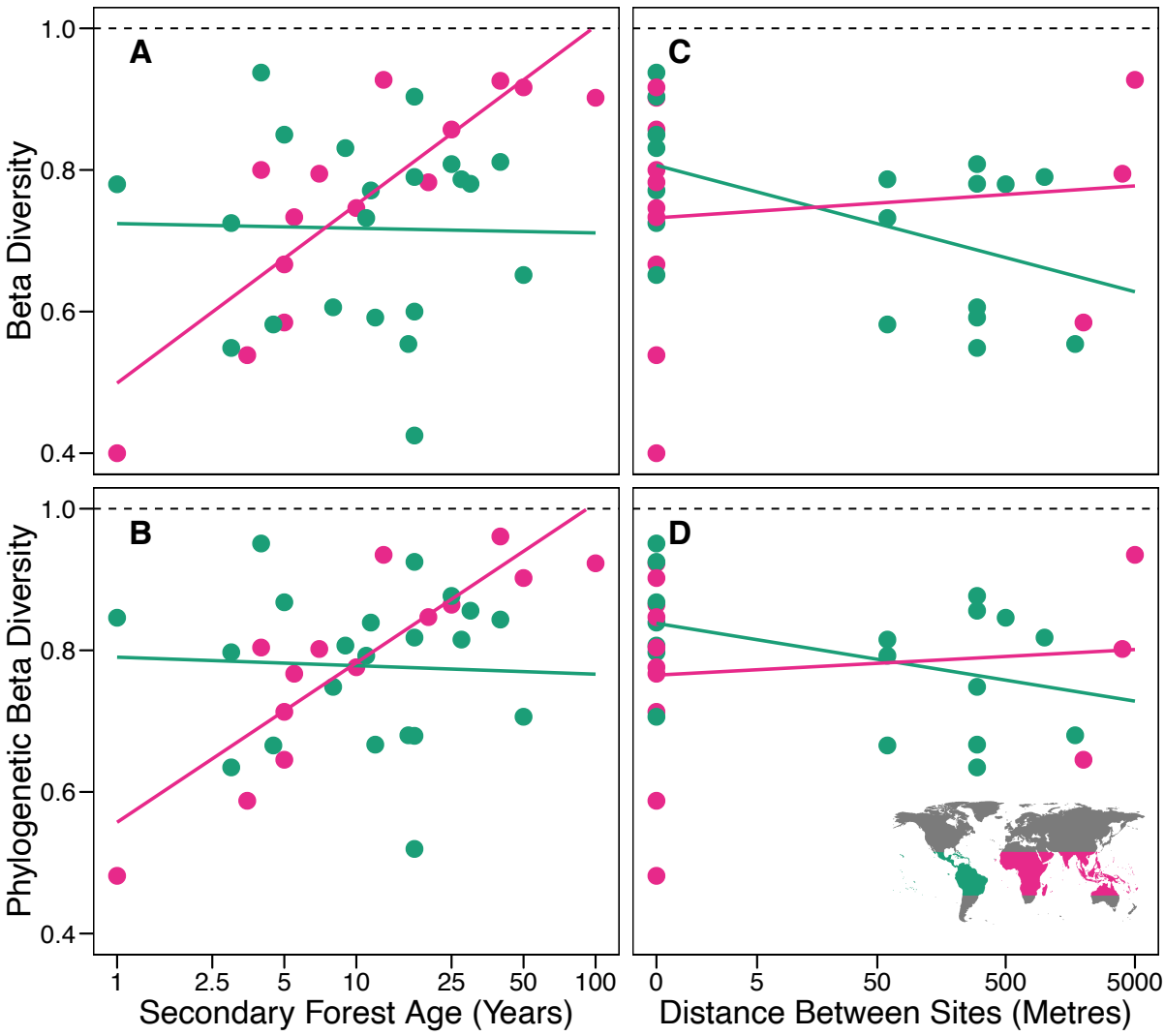

Figure 4.4: The effect of secondary forest age on **A)** *ßTD* and **B)** *ßPD* and the distance between primary and secondary forest sites on **C)** *ßTD* and **D)** *ßPD* in the New World (green) and Old World (pink). Secondary forest age is plotted on a log10 scale. On both y-axes, values fall between 0 (primary and secondary forests are dissimilar) and 1 (primary and secondary forests are similar). Lines of best fit were plotted from the fixed effects output of our mixed effects models. The dotted line represents the value at which primary and secondary forests are identical.

4.4.3 Species and phylogenetic diversity

Across all sites, relative SR did not increase with secondary forest age (LRT: χ^2=2.22, p=0.137). However, in the Old World, as secondary forest age increased relative SR recovered (LRT: χ^2=6.39, p=0.011) and reached primary forest levels in ~46-years (**Figure 4.5A, Appendix 3**

Table S5). As with our analysis of community intactness above, we found a significant but weak interaction between age and distance. Secondary forest age did not have a significant effect on SR in the New World (LRT: χ^2=0.01, p=0.928). We found a positive effect of secondary forest age on PD recovery in the Old World (LRT: χ^2=4.01, p=0.045), with PD reaching primary forest levels ~84-years after disturbance (**Figure 4.5B, Appendix 3 Table S5**). Secondary forest age did not have a significant effect on PD in the New World (LRT: χ^2=0.08, p=0.782). Secondary forest regeneration time had no effect on ses.PD levels in the New World, Old World, or across all sites (**Appendix 3 Table S5**).

Across New World sites, relative ses.MPD decreased as secondary forest age increased (LRT, χ^2=4.40, p=0.040) (**Figure 4.5C, Appendix 3 Table S5**). This indicates that species within communities become more closely related to each other as secondary forest age increases. We found no effect of secondary forest age on ses.MPD in the Old World or across all sites (**Appendix 3 Table S5**). Relative MNTD decreased in the Old World as secondary forests get older (LRT, χ^2=4.31, p=0.038) (**Figure 4.5D, Appendix 3 Table S5**). No change in relative MNTD was found in the New World, or across all sites (**Appendix 3 Table S5**). Secondary forest age did not predict relative MPD, MNTD or ses.MNTD in the New World, Old World, and across all sites, with models containing secondary forest age not significantly explaining the data better than null models. Adding climatic variables to our best fitting age and distance models did not improve model fit for any metric of richness or phylogenetic diversity (**Appendix 3 Table S8**).

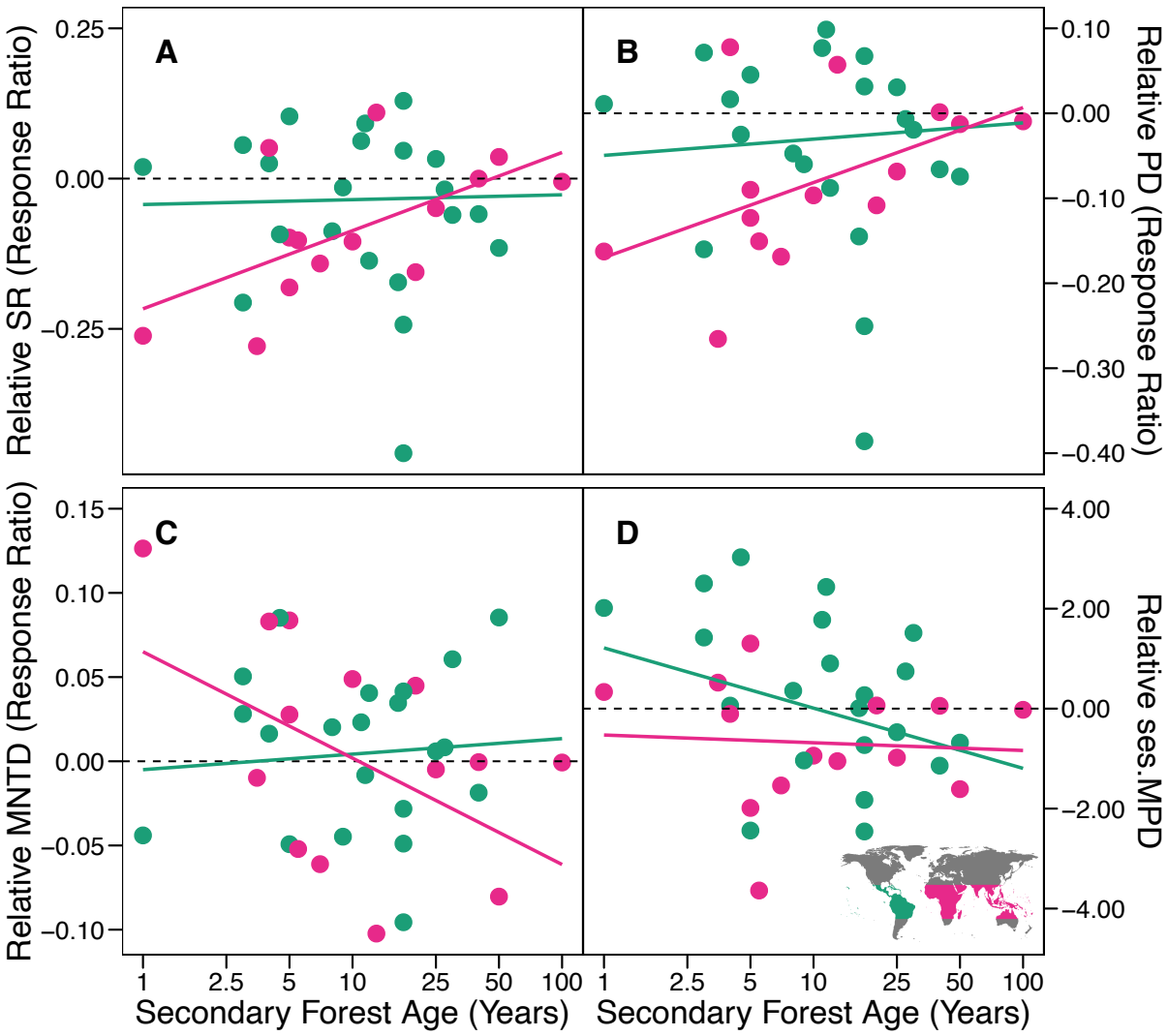

Figure 4.5: The effect of secondary forest age on **A)** relative SR, **B)** relative PD, **C)** relative MNTD and **D)** relative ses.MPD in the New World (green) and Old World (pink). Secondary forest age is plotted on a log10 scale. If SR, PD, MNTD or ses.MPD is lower in secondary forests compared to primary forests, values on the y-axis will be negative and vice versa. Lines of best fit were plotted from the fixed effects output of our mixed effects models. The dotted line highlights where SR, PD, MNTD and ses.MPD are equal in both primary and secondary forests.

4.4.4 Forest dependent species

We found that the relative proportion of forest dependent species increased with secondary forest age across all sites (LRT: χ^2=9.55, p=0.002), New World (LRT: χ^2=4.12, p=0.043), and Old World sites (LRT: χ^2=7.02, p=0.008) (**Figure 4.6, Appendix 3 Table S7**). Indeed, there were

an equal percentage of forest dependent species in paired primary and secondary forest sites in the Old World after 45-years. However, after 50-years of secondary recovery in the New World, there were still 7.7% fewer forest dependent species in secondary forests, compared to primary forests. The proportion of forest-dependent species declined with increasing temperature when temperature was added to the best fitting age and distance model, but only for the New World and global analyses. No other climatic variables improved model fit (**Appendix 3 Table S8**).

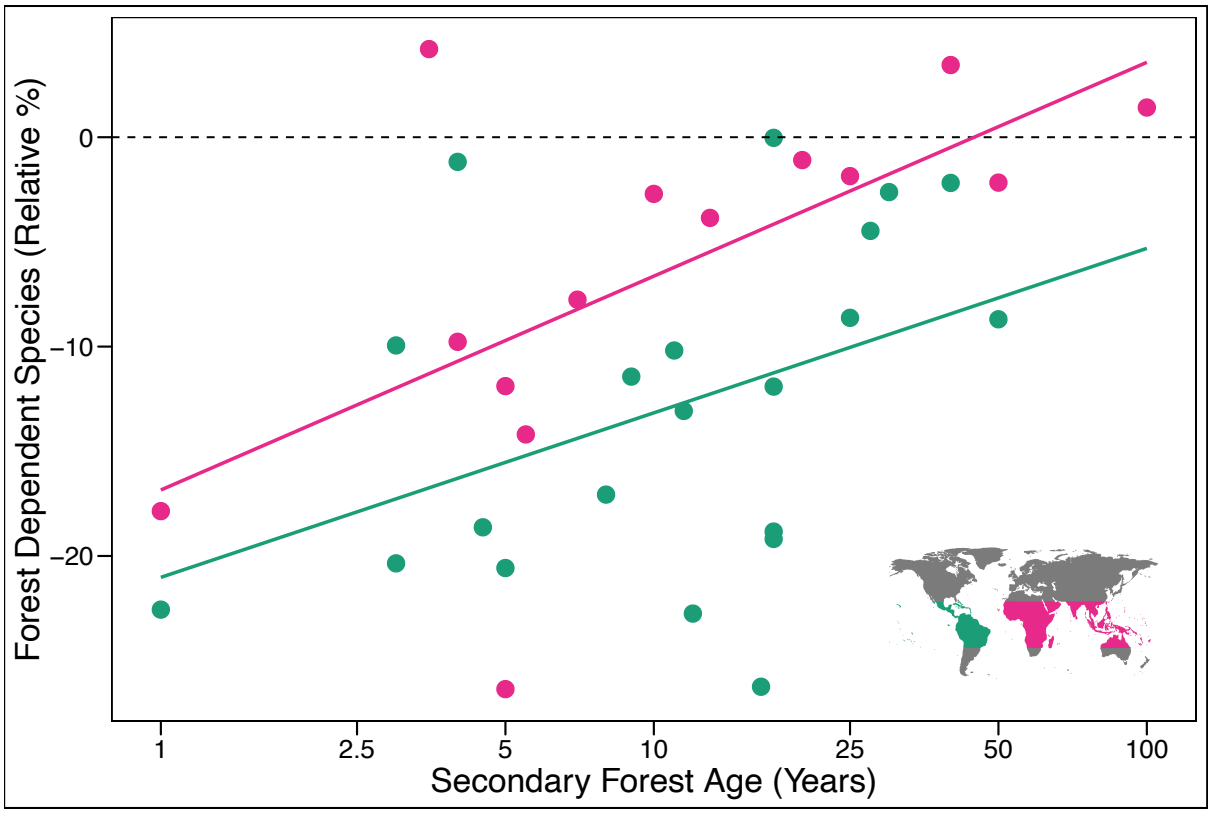

Figure 4.6: The effect of secondary forest age on the proportion of highly dependent forest species found in secondary forest communities when compared to the paired primary forest site in the New World (green) and Old World (pink). Secondary forest age is plotted on a log10 scale. Lines of best fit were plotted from the fixed effects output of our mixed effects models. The dotted line highlights where the proportion of highly dependent forest species in a community are equal in both primary and secondary forests.

4.5 Discussion

Our study represents the first global assessment of recovery of avian phylogenetic diversity in secondary tropical forests. Our results confirm that secondary forests can act as important reservoirs of phylogenetic diversity, particularly in landscapes with little remaining natural forest (Frishkoff et al., 2014). Overall, we find that avian PD recovers towards primary forest levels as Old World secondary forests become older, reaching equivalence at around 100-years, but that this level of recovery is not evident in New World secondary forest. Importantly, this pattern is not driven by the colonization of a closely related set of species, but by the same set of species found in primary forests returning to Old World secondary forests sites over time (as highlighted by increasing community intactness with age). This suggests that, at least in the Old World, forest specialist species that are threatened by forest loss are returning to secondary forests. In New World secondary forests, previous work has shown that both SR (Dunn, 2004) and PD (Edwards et al., 2017) recovers as secondary forest age increases. Our findings from the Old World support the hypothesis that secondary forest regeneration can lead to comparable biodiversity to those found in primary forests and that PD recovers concomitantly with SR as the set of species that colonise secondary forest during recovery is drawn from the primary forest pool.

Previous studies (e.g., Edwards et al. 2017, Frishkoff et al., 2014) found that the conversion of primary forest to agricultural land can initially lead to phylogenetic clustering, with the avian community containing species that are on average much more closely related to each other in evolutionary time. If secondary forest allows recovery of avian communities, then we might expect to see the trend reversed with increasing phylogenetic diversity and decreasing clustering through time. Our results are partially consistent with this prediction but suggest a

more nuanced dynamic of gains of forest species alongside loss of non-forest, open habitat species. In both the Old and New World, the proportion of forest-dependent species increases with secondary forest age, although the effect appears to be weaker in the New World, at least with respect to our sampled sites. In the Old World, this is concomitant with increases in SR and PD. In the New World, neither SR nor PD increase with age.

The degree of phylogenetic clustering, however, appears to increase with age in both the Old World and the New World. This result is best explained by the gradual shift from open/agricultural habitats to mature forest, as opposed to the abrupt change associated with deforestation in the reverse direction. Avian communities in the early stages of recovery are likely to consist of resilient open-habitat species (Acevedo-Charry and Aide, 2019), those from younger clades (Edwards et al., 2017; Frishkoff et al., 2014), species with wide diet breadths (e.g., granivores) (Frishkoff et al., 2014), and the most resilient forest-dependent species. Over time, the gain of forest species seems to outweigh the loss of open habitat species, leading to net gains in SR and total PD (although this was only observed in the Old World in our data). However, the community becomes increasingly dominated by a more closely related set of forest specialists returning and becoming more common (e.g., understory insectivores: Acevedo-Charry and Aide, 2019; Stratford and Stouffer, 2015). This turnover driven pattern is borne-out by considering analyses using species pools including all species compared to species pools with only forest dependent species: the clustering trends are much weaker or absent in analyses including only forest dependent species. If this pattern of recovery continues steadily over time, then we would expect to observe trends that eventually lead to clustering patterns that are similar to those in primary forests. The absence of this pattern in our data suggests that secondary forest may take a longer period of time

than that captured in our data set for to mature. If so, then some of the most forest-dependent species may have not yet returned, and indeed may never return (Acevedo-Charry and Aide, 2019; Sayer et al., 2017). In both our Old and New World samples, species from some clades represented in primary forest do not appear in secondary forest sites and are also among the most phylogenetically distinct, such as Potoos and Sunbittern in the New World and the Nightjars and Frogmouths in the Old World.

While forest species appear to increasingly colonise secondary forest communities over time in both the Old and New World, community composition recovers with age in the Old World but not the New World where paired primary and secondary forests hold 72% of the same species, and this does not significantly change across the 50-year study period. This could be interpreted as evidence for hemispheric differences in the response of species and such differences could be the result of largely independent evolutionary histories. However, we suggest a more parsimonious explanation due to differences in the sites included in our meta data set. Specifically, in the Old World, the majority of paired sites are contiguous such that secondary forest abuts primary forest. Only three sites in our Old World data are not connected (and are also the most distant sites within the entire data set). Effectively, and by chance, this controls for potential confounding effects of distance and the role of species-specific dispersal in determining patterns of recovery. In contrast, New World sites are rarely contiguous and distances between secondary and primary forest sites are highly variable (ranging from 0-1725 metres). Indeed, our models including distance between sites suggested lower recovery as distance increases. That is, in the New World recovery by distance may mask any effect of recovery by age. We are cautious in our interpretation because the distance data is incomplete and, in some cases, qualitative rather than quantitative.

An alternative explanation for our finding that PD recovery differs in the Old and New World could be a difference in species dispersal potential. Moore et al. (2008) found that some Neotropical species in Panama were unable to fly 100 meters, and similarly, passerines from the families Formicariidae and Thamnophilidae in the Brazilian Amazon failed to cross 250 meters over farmland to reach their territories (Laurance and Gomez, 2005). While bird groups with poor dispersal ability, such as the wren-babblers (Timallidae), do occur in the Old World there may be disproportionately more poorly dispersing species in the New World. At present, detailed data on the dispersal ability of many tropical birds are lacking. Nonetheless, identifying whether New World species share any dispersal, or colonisation, limiting traits could suggest that region-and ecology-specific conservation strategies are required for secondary forest management.

4.6 Conclusions

4.6.1 Management Implications

The rate of deforestation of primary tropical forests is unlikely to slow. In some regions that have experienced high levels of primary forest loss in agriculturally suitable areas, the area of space occupied by secondary forests is increasing as farmland is abandoned. For instance, in Latin America and the Caribbean, >360,000km^2 of new secondary growth occurred between 2001 and 2010 (Aide et al., 2013). Furthermore, each year around 290,000km^2 of secondary forest regrowth occurs on abandoned land globally (Hurtt et al., 2017). Abandonment is most likely to happen in marginal areas that are too dry or steep for more modern farming methods (de Rezende et al., 2015; Sloan et al., 2016), and it is these areas that perhaps pose the biggest opportunities for conservation gains (Edwards et al., 2017; Gilroy et al., 2014).

Forest connectivity, the sizes of primary forest patches, and human activity, could influence the rate at which species can re-colonise secondary forests following abandonment (Banks-Leite et al., 2012; Maldonado-Coelho and Marini, 2000; Prugh et al., 2008). The majority of secondary forests are reportedly found in close proximity to remnant forest across the tropics (Crk et al., 2009; Edwards et al., 2017; Sloan et al., 2016), and it is therefore likely that primary forest patches acted as sources of colonizing dispersers to secondary forest patches across all sites in our study (Gilroy and Edwards, 2017). Indeed, in the Old World, the majority of secondary forest sites are contiguous with primary forest sites.

Although secondary forest regeneration is likely to occur in areas that are unsuitable for modern farming practices, they still face the threat of deforestation. Indeed, in Costa Rica 50% of secondary forests were found to have been cleared within 20-years, and 84% within 54-years (Reid et al., 2018). In both the Old and New World, using carbon-based payments for ecosystem services under REDD+ to protect these new forests from deforestation or to enhance the rate with which land is abandoned and returned to secondary forest (Gilroy et al., 2014) represents a key conservation opportunity. Furthermore, the emerging global Forest and Landscape Restoration agenda, in which nations have targeted 350 million hectares of restoration by 2030 (“Bonn Challenge,” n.d.; “GPFLR,” 2003) represents another policy driver for the recovery of secondary forests. Such investments should be focused on land in close proximity to primary forests, which our study suggests would enhance the rate of recovery of diversity. In addition, regenerating forests tend to be poorly protected, with laws, policies and socioeconomic conditions that can work against long-term persistence. In Costa Rica, for example, the laws that protect forests exclude young, regenerating sites; in

fact, they are often targeted for clearing to prevent them being reclassified as forest (Sierra and Russman, 2006). We thus need to focus our attention on legal frameworks to remove disincentives to the longer-term persistence of secondary forests.

Taken together, our results point to an important role of secondary forest in maintaining tropical forest biodiversity, but also suggest the critical need to provide long-term management and protection to maximize conservation benefits. We also highlight the importance of integrating local and regional patterns of fragmentation and landscape ecology when investigating the potential of secondary forests to safeguard biodiversity (Arroyo-Rodríguez et al., 2017). Secondary forests are likely to be at constant threat of reconversion to farmland (Reid et al., 2018; Sánchez-Cuervo and Aide, 2013; Sodhi et al., 2010) and given that agricultural land has far lower SR and PD than does secondary forest (Edwards et al., 2017), protection of secondary forests should be seen as a priority for the conservation of tropical biodiversity.

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CHAPTER 5

General Discussion

5.1 Biodiversity and global change

Exploring and understanding the biogeographic patterns of biodiversity are central in determining its origins, and in the face of global change, its conservation. Biodiversity is often measured by calculating species richness, which ignores the potential importance of individual variation in species traits, features, and evolutionary history. In this Thesis, I used trait and phylogenetic diversity metrics to interrogate global scale biogeographic patterns of avian diversity, assess the impact of species extinctions on this diversity, investigate more local effects of recovery following land-use change, and reviewed implications for conservation. In the general introduction (**Chapter 1**), I identified the following key outstanding questions.

i) How is trait diversity distributed globally?

ii) Do species extinctions lead to homogenisation of trait and phylogenetic diversity?

iii) Can phylogenetic diversity recover after land-use change?

Here, I summarise the main answers to these research questions, before highlighting and discussing implications and future directions relating to these findings.

5.2 Global distribution of trait diversity

In **Chapter 2**, I presented the first global mapping of a suite of ecologically relevant, continuous, morphological traits, complementing previous research on the drivers and

patterns of terrestrial global avian diversity (Voskamp et al., 2017), and my own observations of higher and lower than expected phylogenetic diversity across the whole avian class (**Figure 1.1**). I measured how species fill morphospace in two ways, by capturing the spread and density of species to reveal that evolutionarily old species likely contribute to niche expansion, and young, rapidly speciating species to niche expansion in the highly productive tropics. My findings add to evidence suggesting that the tropics are both 'museums' and 'cradles' of biodiversity (Gaston and Blackburn, 1996; Jablonski et al., 2006; McKenna and Farrell, 2006; Rolland et al., 2014).

Contemporary environment is often argued to have had a strong role in shaping global patterns of species richness (Safi et al., 2011), for example, heterogenous habitats are thought to lead to greater species coexistence through increased niche availability, and higher productivity leads to increased resources and a reduction in the ecological limits constraining species coexistence (Davies et al., 2007; Kerr et al., 2001; Kerr and Packer, 1997; MacArthur and MacArthur, 1961; Rahbek and Graves, 2001). In contrast, I find only weak support for primary productivity driving dense packing of trait space, and no effect of habitat type or heterogeneity. Overall, my research implies that evolutionary and biogeographic history have left a lasting imprint on extant avian assemblage structure, specifically with respect to the types of species rather than just the number of species, to a much greater extent than contemporary environmental variables.

5.3 Extinction and homogenisation

Keeping the focus on broad spatial scales, in **Chapter 3** I examined whether the loss of sequentially more threatened bird species would lead to a significantly greater loss of trait

and phylogenetic diversity than predicted (Oliveira et al., 2020). These measures are particularly sensitive to the non-random loss of species (Cardillo et al., 2005), and can therefore be used to identify where extinction of threatened species could lead to biotic homogenisation (Clavel et al., 2011; Daru et al., 2021; McKinney and Lockwood, 1999). Across the whole class, I found a clear impact of morphological homogenisation, with bird species within communities becoming more similar on average in terms of their morphology. This finding builds upon previous work by Cooke et al., (2019a), who found that avian extinctions will lead to an ecological downsizing of species, as well as a shift towards "faster" life history strategies. Avian extinctions are therefore predicted to lead to the homogenisation of both morphological (**Chapter 3**) and life-history diversity (Cook et al., 2019a) across the avian Class.

This pattern plays out spatially, with the majority of biomes and ecoregions containing assemblages that will become significantly morphologically homogenised as threatened species become extinct. Areas at the most risk are those found in East Asia, particularly the Himalayan upland and foothills, where I identified assemblages as being particularly densely packed in niche space (with low spread and high density) in **Chapter 2**. In contrast, I found expected declines in phylogenetic diversity given the loss of species across the entire class, and for the majority of biome and ecoregion assemblages. This is despite finding that extant avian morphological and phylogenetic diversity correlate strongly, and that there is strong phylogenetic signal in the traits we used, although deviations from strict Brownian motion are prevalent (Chira et al., 2018; Cooney et al., 2017).

5.4 Recovery after land-use change

Conversion of pristine habitat for human use is the biggest driver of the biodiversity crisis, and this is most acute in tropical rainforests (Laurance et al., 2014). However, in many areas, high rates of agricultural land abandonment in the tropics have led to the widespread growth of secondary forests (Aide et al., 2013; Hurtt et al., 2017; de Rezende et al., 2015; Sloan et al., 2006), which present a unique opportunity for safeguarding biodiversity (Aide et al., 2013; Edwards et al., 2017; Frishkoff et al., 2014; Gilroy et al., 2014). In **Chapter 4**, I focused on local scales, at sites in the Old and New World, and assessed whether regenerating secondary forests could provide opportunity for the phylogenetic diversity of communities to recover to comparable primary forest levels (Edwards et al., 2017).

In Old World tropical forests, phylogenetic diversity recovers to primary forest levels as secondary forest age increases, and this is driven by the same species returning, including vulnerable forest specialist species. In the New World, this recovery is not seen, and may be because of the confounding effect of distance to primary forest (Banks-Leite et al., 2012; Maldonado-Coelho & Marini, 2000; Prugh et al., 2008), or fundamental differences in the ecology of New and Old World forest birds, such as lower dispersal abilities (Laurance and Gomez, 2005; Moore et al., 2008), or decreased resilience to disturbance. I conclude that there remains a critical need to provide long term management and protection of secondary forests, particularly those contiguous to primary forests (Gilroy and Edwards, 2017), in order to maximise conservation benefits.

5.5 Global versus local scale

In this Thesis, I employ a variety of different scales to move from global and regional biogeographical contexts in **Chapters 2 and 3**, to a more local, conservation focus in **Chapter 4.** The use of multiple scales allows additional insight into the origins and drivers of extant biodiversity patterns. For example, in **Chapter 2**, at the global level, I find dense packing of species in morphological trait space, and at the regional level, high morphological variance – species fill a wide area of trait space. My analysis reveals that these patterns of morphological diversity in the tropics carry signatures of evolutionary history – young species contribute to niche packing and older species contribute to niche expansion – showing that the tropics are both 'museums' and 'cradles' of diversity (Gaston and Blackburn, 1996; Jablonski et al., 2006; McKenna and Farrell, 2006; Rolland et al., 2014).

In **Chapters 2 and 3**, I used species distribution maps (http://www.birdlife.org/datazone/home) projected onto 100km and 50km grid-cell resolutions to assess global patterns of morphological trait diversity and the homogenisation of phylogenetic and morphological diversity. Due to the quality of range maps, reducing spatial graining to a finer resolution would be problematic (Hurlbert and Jetz, 2007). An advantage to using these maps is that despite being less accurate and lacking species abundance data, they do allow for a much broader scope across the whole globe including filling gaps in regions where survey data are missing, not adequately plentiful or still being acquired (Chaplin-Kramer et al., 2022; Hughes et al., 2022). However, it is likely that in some instances we are overestimating the occurrence of certain species in areas where they have already become locally extinct, and this could mean we are, for example, underestimating homogenisation in these ecoregions (**Chapter 3**).

The scale used in any spatial analysis is particularly important as it clearly impacts the inferences that can be made. For example, effective local-scale conservation cannot directly be informed by global scale patterns (Chaplin-Kramer et al., 2022; Wyborn and Evans, 2021). However, global mapping can provide important context for local decision making, and an integrated approach from local to regional to global scales enables the impacts of policies or actions to be assessed more widely (Chaplin-Kramer et al., 2022). In addition, only setting conservation strategies at a local scale without wider considerations of its impacts in mind, can conflict with national or global goals to protect globally endangered species or ecosystems (Chaplin-Kramer et al., 2022; Wolff et al., 2020). Global mapping can also highlight knowledge gaps, including areas of the globe that would potentially benefit from increased investment in conservation, such as the bird communities of the tropical moist forest and grassland areas of Southern Indochina (e.g., Vietnam, Cambodia) highlighted by my findings in **Chapter 3**.

5.6 The conservation of tropical avian morphological and phylogenetic diversity

Tropical moist forests are the biome most intensely threatened by continued conversion for Anthropogenic land-uses such as agriculture (Gibbs et al., 2010; Hansen et al., 2013; Laurance et al., 2014). Combined with the fact that tropical rainforests contain the most hyper-diverse species assemblages, and account for half of all carbon stored in vegetation on the planet (Lewis et al., 2015), the conservation of tropical ecosystems is a global conservation priority. Birds perform many important ecosystem functions in tropical rainforests, including, for example, seed dispersal and pollination (Şekercioğlu et al., 2016). Indeed, the current declines of frugivores could have major consequences for seedling dispersal and recruitment and

therefore forest carbon storage (Bello et al., 2015; Brodie et al., 2021; Chanthorn et al., 2019; Rogers et al., 2021).

The threat of morphological, as well as phylogenetic homogenisation is particularly acute in tropical forest ecoregions across Central Africa, Central America, and South America, as well as Indochina and Southeast Asia (**Chapter 3**) where the majority of recent deforestation hotspots can be found (Lewis et al., 2015). In **Chapter 4**, I highlighted that protecting secondary forests (naturally regenerating forests on abandoned land) should be seen as a critical priority for the conservation of tropical biodiversity given that they can recover comparable levels of phylogenetic diversity to primary forests (Edwards et al., 2017; Hughes et al., 2020). This is particularly important as community recovery can take many decades post-disturbance (Acevedo-Charry & Aide, 2019; Dunn, 2004; Poorter et al., 2021; Sayer et al., 2017) and secondary forests are at near constant threat of reconversion to farmland, even targeted to prevent them being reclassified as forest (Reid et al., 2018; Sanchez-Cuervo & Aide, 2013; Sierra and Russman, 2006; Sodhi et al., 2010).

Using carbon-based payments for ecosystem services under REDD+ to encourage new, and to protect existing secondary forests represents a key opportunity (Gilroy et al., 2014), as do contributions to forest restoration as part of the global Forest and Landscape Restoration agenda (Bonn Challenge, n.d.; GPFLR, 2003). Forest carbon projects have many co-benefits for society, providing essential contributions to people by supporting dietary needs through increased pollination services for pollinator-dependent agriculture, improved water quality, and safeguarding biodiversity (Gilroy et al., 2014; Sarira et al., 2022). For example, in South-East Asia, where tropical forests are amongst those most threatened by phylogenetic and trait

homogenisation (**Chapter 3**), 58% of existing forests that are threatened with deforestation represent financially viable carbon projects and would protect 25 million hectares of Key Biodiversity Areas (Sarira et al., 2022). Given these benefits, there is clearly a need for legal frameworks to remove disincentives to enable the longer-term persistence of secondary forests.

5.7 Linking morphological traits to ecosystem functioning

The lack of use of trait and phylogenetic diversity measures when setting priorities and policies for conservation is clear (Devictor et al., 2010; Veron et al., 2017). In part this may be because high-quality global trait datasets, and phylogenies, are relatively new for whole taxonomic groups, and still absent for others. More crucially, it is not currently well-defined, for most taxa, whether measurable species traits can capture features of conservation priority, such as key ecosystem services, better than other measures of biodiversity (Flynn et al., 2011; Philpott et al., 2009). Conserving ecosystem functions are a top priority as human well-being, and indeed survival, depends on the ecosystem goods and services they deliver.

It is often stated that measuring species trait diversity is one of the best predictors of ecological niche and function in ecosystems (Diaz and Cabido, 2001; Petchey and Gaston, 2006). Communities with high trait diversity partition resources more than low trait diversity communities, leading to higher ecosystem functioning (Cadotte et al., 2011). Whilst relationships between traits and services have been examined across multiple taxa, the field is dominated by research regarding plant communities (Cadotte et al., 2011; de Bello et al., 2010; Luck et al., 2012).

Explicitly testing the link between trait diversity and ecosystem function is challenging, however conclusions from research in grassland plant communities found that the diversity (i.e., functional (trait) richness), and composition of traits better predicted ecosystem functioning than species richness (Tilman et al., 1997). Further research found that multivariate metrics of trait diversity performed better still (Petchey et al., 2004). Furthermore, functional (trait) richness has also been found to perform worse than all other biodiversity measures at predicting ecosystem functioning (Flynn et al., 2011) with functional trait identity and divergence performing better (Mouillot et al., 2011), suggesting that the metrics used are an important consideration alongside trait selection. More recently, the individual effects of grassland plant species on ecosystem services have been explored, allowing the identification of keystone species that have most influence on the relationship (Brun et al., 2022). Furthermore, functionally distinct species that exhibit unique combinations of traits are important for long-term productivity in extreme environments (Delalandre et al., 2022). Conserving such species could be seen as a conservation priority and is an interesting direction for future research in other taxa and ecosystems.

Birds are important components of ecosystems and their functioning (Şekercioğlu et al., 2016), however, our knowledge of how avian traits map to ecosystem services is limited, and in some cases species richness has been found to be a better predictor (e.g., Philpott et al., 2009). Nonetheless, large gains in the number of novel, high-quality trait datasets (e.g. 3D beak shape (Chira et al., 2018; Cooney et al., 2017; Hughes et al., 2022), Kipp's distance (Sheard et al., 2020; Tobias et al., 2022), plumage colouration (Cooney et al., 2019) etc.) over recent years, means there is now excellent global coverage across the entire avian class. Furthermore, the development of easy-to-use computational tools has made calculating a

range of trait diversity metrics straight forwards (e.g., Guillerme et al., 2020a, 2020b; Magneville et al., 2022). An outstanding area of research therefore is formalising links between bird species trait diversity and ecosystem services.

Throughout this Thesis, I use a suite of morphological traits, including a unique dataset of 3D bill shape. The avian bill has evolved into a huge array of forms, from the long, slender bills of hummingbirds (Trochilidae) to the elaborate casqued bills of hornbills (Bucerotidae), the flat, dabbling bills of some ducks (Anatidae), and the deep, chunky beaks of finches (Fringillidae), to everything in-between. In turn, this vast diversity of bill shapes allows birds to exploit certain food types. A classic example of how beak shape maps to ecological function is in Darwin's *Geospiza* finches (Grant and Grant, 2006), with each species having beak shapes linked to the types of seeds on which they feed.

Figure 5.1: Violet Sabrewing (*Campylopterus hemileucurus*) Male. 25th March 2022, Costa Rica.

Nonetheless, beak shape does not always map directly to foraging niche (Navalón et al., 2019), especially because similar functional roles can be achieved through multiple phenotypes (Bright et al., 2016; Miller et al., 2017). Furthermore, the bill is an important tool for other tasks (e.g., preening (Moyer et al., 2002), nest building (Hansell, 2000), sexual signalling (Navarro et al., 2009) etc.), and so foraging ecology is unlikely to explain all variation in bill shape. Indeed, Navalón et al. (2019) quantitatively tested this using regression analysis and found that diet only predicts 12% of bill shape variation across the avian class. However, when increasing the number of traits considered to include additional traits such as tarsus and wing length, Pigot et al., (2020) found that avian morphology plots with 70-85% accuracy onto major trophic niche axes, and that this is driven by convergent evolution towards predictable trait combinations. In order for avian trait diversity to be more clearly considered option for conservation, there is a crucial need to extend existing research to link avian traits more directly to ecosystem services.

5.8 Other types of traits

My choice to use morphological traits (i.e., beak shape and size, body size, tarsus and wing length) when calculating trait diversity metrics in **Chapters 2** and **3** was driven by both their similarity to those linked to avian ecological foraging guilds (Pigot et al., 2020, and also because they are continuous data of high-quality that cover the vast majority of species globally. Furthermore, prior to commencing, and during my PhD studentship, I was heavily involved in collecting and curating the novel 3D beak shape dataset under an ERC grant on which my supervisor Dr Gavin Thomas was Principal Investigator, giving me access to and knowledge of the data. My choice of traits was therefore a pragmatic one. As outlined in the previous section, proven links between these sorts of traits and ecosystem functioning are

currently lacking (Luck et al., 2012), which means subjective decisions are often made as to which aspects of species phenotypes are most important to conserve. Despite this, using morphological traits allowed me to make important inferences in **Chapter 4**, such as identifying the ecological guild of species that are driving patterns of morphological homogenisation in the Himalayas (e.g., large obligate scavengers). These traits also revealed how species fill niche space across the globe in **Chapter 2**, building on iconic work by MacArthur and MacArthur (1961). Nonetheless, a plethora of different morphological and behavioural traits are available that could provide different insights into global biogeographic patterns (e.g., Sheard et al., 2020) and could equally be justified as important to conserve.

The life histories of organisms are a key component of phenotypic variation and explaining this variation has long been a central goal for ecologists and evolutionary biologists (Stearns, 1983). Species exist along a fast-slow continuum with those living "fast" by reproducing quickly, and having higher mortality etc., and those that live "slow" by maturing late, reproducing slowly, and living longer etc. (Bennett and Owens, 2002; Sæther, 1987). Species with slow life histories are often found to be at increased risk of extinction, due to their low reproductive rates, and their tendencies towards larger body sizes (Cooke et al., 2019a). Traits such as litter/clutch size and generation length, are often used to represent species reproductive rates and life history (Carmona et al., 2021; Cooke et al., 2019a), which are readily available (e.g., Myhrvold et al., 2015; Oliveira et al., 2017).

An exciting area of current life history research is that involving reproductive success in birds (Hemmings and Evans, 2020). For example, current research led by PhD student Fay Morland and Dr Nicola Hemmings at the University of Sheffield is investigating high levels of infertility

and prenatal mortality in the Hihi (*Notiomystis cincta*), which is threatened by extinction. The reduction of hatching failure is a key management strategy to conserve endangered species (Marshall et al., 2021) and can account for individual level differences in fertility. A key outstanding question is whether fertility could be used in trait diversity metrics to identify species that are likely to be most threatened with extinction in the future.

Another characteristic of birds is that they are the most strikingly colourful land vertebrates and so exhibit a huge diversity of feather colour (**Figure 5.1**) (Stoddard and Prum, 2011). The beauty of birds' plumage has inspired many throughout human history, but it has unfortunately also made them the target of trapping, shooting, and collecting by humans. The rush to collect specimens to meet the desire for colourful feathers for women's fashion during the Victorian Era, contributed to the catastrophic population declines of many bird species (Moore-Colyer, 2000). Today, despite protection under the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES), thousands of threatened and non-threatened vertebrate species are traded commercially each year (Morton et al., 2022). Understanding the traits of species most likely to be traded could help inform conservation protocols aimed at minimising species declines. A large, comprehensive, high-resolution dataset of avian colourfulness data now exists (Cooney et al., 2019), and it is traits such as this that could potentially be useful in assessing whether more phenotypically unique species tend to be more traded and indeed, have higher extinction risks. Many avenues for future research are now available to scientists given the increasing availability of trait data, and at finer resolutions than ever before (i.e., at the intraspecific level).

Figure 5.2: Examples of the rich diversity of avian plumage colouration. Top row, left to right: Golden-fronted leafbird (*Chloropsis aurifrons*), White's Thrush (*Zoothera aurea*), Scarlet-rumped Trogon (*Harpactes davaucelii*). Middle row, left to right: Mrs Gould's Sunbird (*Aethopyga gouldiae*), Abyssinian Roller (*Coracias abyssinicus*), Greater Blue-eared Starling (*Lamprotornis chalybaeus*). Bottom row, left to right: Black-naped Monarch (*Hypothymis azurea*), Galah (*Eolophus roseicapilla*), Bar-bellied Pitta (*Hydrornis elliotii*).

5.9 Implications for measuring trait diversity

To quantify trait diversity, a plethora of metrics exist that aim to capture different aspects of how species are distributed across multidimensional trait space (Guillerme et al., 2020b;

Laliberté and Legendre, 2010; Laureto et al., 2015; Pavoine and Bonsall, 2011; Villéger et al., 2008). In **Chapter 2**, I used two metrics to quantify multidimensional trait space as using single metrics limits the inferences that can be made (Guillerme et al., 2020b; Villéger et al., 2008). For example, my finding of exceptionally high density (species are close to their nearest neighbour) and spread (species occupy a wide area of trait space) of species in Northern temperate regions can only arise if clusters of morphologically similar species occupy trait space. Looking at a single metric would have indicated quite different conclusions (i.e., high spread indicates niche expansion, high density indicates niche packing). My research further shed light on the finding by Cooke et al., (2019b) that bird assemblages in Northern polar and temperate biomes tend to exhibit higher than expected dispersion of traits (Cooke et al., 2019b).

Furthermore, trait diversity metrics can capture multiple aspects of species occupancy in trait space, and so implementing simulations to visualise and capture this seems a crucial (but mostly lacking) approach when choosing which metrics are best to use for a given study (Guillerme et al., 2020a). For instance, the commonly used Functional Dispersion metric or average Euclidean distance from the centroid of morphospace (Anderson, 2006; Laliberté and Legendre, 2010), can strongly capture the size of morphospace, and somewhat the density of species within trait space (Guillerme et al., 2020b). Therefore, I used simulations of species losses and gains, to test exactly how a variety of trait diversity metrics captured changes in morphospace volume and density to inform my selection of metrics for **Chapters 2** and **3** (Guillerme, 2018; Guillerme et al., 2020b). Given this, researchers should ensure the careful selection of trait diversity metrics and understand how they capture multidimensional trait

space, especially as computational tools to aid this are readily available (e.g., Guillerme, 2018; Guillerme et al., 2020b; Magneville et al., 2022).

5.10 The increasing availability of data

The increasing availability of global trait databases means that the variation in avian traits can be quantified at a variety of spatial and taxonomic scales and can be used, for example, to understand the biogeographic patterns of biodiversity, the functioning of ecosystems, the impacts of species extinction, and to inform conservation managements strategies (Cooke et al., 2019a, 2019b; Edwards et al., 2021; Pigot et al., 2016; Sayer et al., 2017; Sheard et al., 2020; Tobias et al., 2020).

Natural history collections have been a hugely vital resource in the creation of large-scale trait datasets, with between 1.2 and 2.1 billion specimens thought to exist worldwide (Ariño, 2010). The global diversity of extant bird species is exceptionally well represented in Museum collections, with the largest individual collections housing over 95% of species diversity (e.g., Natural History Museum, Tring, UK; American Museum of Natural History). Nonetheless, gaps do exist for rarer or cryptic taxonomic groups, for geographically harder to access places, and for females due to sex-biases in collecting (Cooper et al., 2019; Etard et al., 2020). Although there is unlikely to be strong phylogenetic and spatial biases, for our trait dataset some species are missing, and so some bias could exist. This could mean, for example, that our results are underestimating niche packing in high richness areas. Furthermore, the vast majority of natural history collections are not digitised in any form. In order to unlock the maximum potential of these historical collections, digitisation is a key, ongoing, priority for curatorial research.

Whilst trait datasets for birds are amongst the most detailed in terms of their quality, geographic and phylogenetic coverage when compared to other taxa, a clear limitation is that most datasets are averaged at the species level (Cooney et al., 2017; Oliveira et al., 2017; Tobias et al., 2022). Phenotypic variation amongst individuals has long been observed and can vary between the sexes (Shine, 1989), and even change over an individual's lifetime depending on feeding behaviour, like the bill shape of the oystercatcher (Swennen et al., 1983). A key area for future research therefore is to quantitatively sample intraspecific variation in traits, to complement interspecific trait data and help bridge the gap between macro-, and micro-evolutionary processes. In addition, the rapid expansion of molecular datasets, including the Bird 10,000 Genomes Project which aims to sequence the genomes of all extant bird species (Feng et al., 2020), will enable improved knowledge on the phylogenetic relationships between taxa, as well as the genetic basis of avian traits (Lawson and Petren, 2017). Overall, the increasing availability of biological data, from inter-specific traits to genes, opens exciting new avenues and future directions for multidimensional research into the future of avian biological diversity.

5.11 Conclusions

In this Thesis I examined extant and future biogeographic patterns of avian diversity from broad to local spatial scales. By combining novel datasets of avian traits with the avian phylogeny, I have shown that global trends in species richness can be explained by the filling and packing of ecological niche space. In a rapidly changing world, the conservation of the evolutionary history, morphology, and ecological roles that species represent is of critical importance, particularly given my findings that the biodiversity extinction crisis will result in

far greater losses of trait, and in some cases, phylogenetic diversity, than predicted through species loss alone. The fact that phylogenetic diversity can and does recover at local scales in the habitat most threatened by Anthropogenic land-use change, signals hope that the worst of the crisis can be avoided if opportunities for legal frameworks and management strategies to protect existing and recovering and habitats are quickly, and strongly acted upon. Whilst much remains to be discovered, particularly regarding the links between avian morphological diversity and ecosystem functioning, the findings in this Thesis help to further our understanding of the origins of biodiversity, and in the face of global change, its conservation.

5.12 References

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APPENDIX 1

Supplementary materials and methods for Chapter 2:

Global biogeographic patterns of avian morphological diversity.

Section 1: Additional methodology.

a) ***Morphological Trait Data:*** *Further information on the post processing and landmarking of beak shape dataset.*

b) ***Spatial Data:*** *Taxonomy matching and species range maps.*

c) ***Defining Phyloregions.***

d) ***Environmental Correlates.***

a) Morphological Trait Data

We took 3D scans of the beaks of study skins from the bird collections at The Natural History Museum at Tring, Manchester Museum and The Field Museum of Natural History, Chicago, using white and blue structured light scanning (*FlexScan3D*). We selected adult, preferentially male specimens, in part due to sex biases in Natural History collections (Cooper *et al.* 2019), where the beak was intact and all sides and edges of the beak were clear from obstructions.

For each beak, we obtained 5-25 scans that were aligned, and combined using FlexScan3D software (LMI Technologies, Vancouver, Canada). The 3D scans were cleaned (e.g. holes, feathers, obstructions and high aspect ratio spikes were removed), and decimated (the number of faces were reduced to 500,000) using Geomagic Studios (3DSystems). Cleaned

scans were then uploaded to http://wwww.MarkMyBird.org - a bespoke crowd-sourcing website. We used landmark based geometric analysis to measure bill shape. Using the MarkMyBird interface, homologous key points (landmarks) were placed on each of the bill scans. In total, 4 landmarks were placed on 1) the tip of the upper beak, the posterior margin of the upper beak on 2) the dorsal midline (where the beak meets the feathers), 3) the left, and 4) the right tomial edges. Once these four landmarks were placed, 75 semi-landmarks were generated connecting the landmarks together, such that the dorsal profile (landmark 1 to 2), the left, and right tomial edges (landmarks 1 to 3, and 1 to 4 respectively) were defined by 25 equally spaced semi-landmarks. Each bill was 'marked-up' by at least three independent users. R scripts were run to ensure that the mark-ups were of good quality. Mark-ups were removed if 1) the left and right tomial edges were placed asymmetrically or swapped, 2) the semi-landmarks along those edges were not placed in the correct order, or did not follow the curve of the bill, and 3) there was a large discrepancy in the placement of homologous landmarks between different users (Procrustes distance ≥ 0.2).]]

We applied geometric morphometrics using the procSym function in the R package Morpho (Schlager, 2017) to calculate a multidimensional morphospace. First, we conducted a generalised procustes alignment (GPA) for landmark replicates within species to calculate a mean shape for each species. We enforced symmetry (without size scaling) on all species where there is no known asymmetry. Exceptions are the genus *Loxia* (crossbills) and *Anarhynchus frontalis* (wrybill) which have laterally decurved bills. We used the species-level GPA-aligned mean shapes as input for the interspecific GPA of all species. We conducted the interspecific GPA in two steps. In step one we run a GPA and enforce symmetry. This is because landmarker error, even when averaged across users, can result in the false inference

of asymmetry if the positions of the rear tomial edge landmarks are slightly misaligned. In step two we repeat the GPA using the global alignment but replace landmarks of *Loxia* and *Anarhynchus frontalis* with the original intraspecific mean shape. This two-step process ensures that biological asymmetry is accounted for while the effects of false asymmetry are removed. The procSym applies a Principal Component Analysis to the procrustes aligned coordinates and outputs PC scores and centroid size for each species.

b) Spatial Data

i) *Taxonomy matching*

Where a species was considered under a single name in BirdTree, but under multiple names in the BirdLife range maps, we lumped the distribution maps together. If a species was classified under a single species name by BirdLife, but was known across multiple names in BirdTree, we manually split the range polygons using QGIS version: 3.10.2-A (QGIS.org 2020) and descriptions from Avibase (https://avibase.bsc-eoc.org), Map of Life (https://mol.org/) (Jetz et al., 2012a) and HBW (https://www.hbw.com/), where possible. For several species this was not possible, and these along with certain newly discovered, or no longer recognized taxa, were excluded from analysis.

ii) *Species range maps*

Species breeding and resident range maps were included for extant and probably extant species where these species were classified as native and or re-introduced, resulting in species distribution maps for 9932 species selected and matched to the BirdTree taxonomy. Range data were transferred to a 100 km x 100 km equal area grid under a Behrman cylindrical equal-area projection, and species presence or absence in each terrestrial grid cell was recorded. A spatial graining of 100 km was chosen as finer graining is problematic due to

range map quality (Hurlbert & Jetz 2007). Species were considered present in a terrestrial grid cell if approximately 1% or more of their range overlaps (n=9794). To assess this, each grid cell was divided into 100 equally sized squares, and a species was considered present if its range map crossed the centroid of one of these smaller squares.

Species were removed from the presence/ absence matrix where trait data were missing, and grid cells with 8 or fewer species were not included in our analysis (volume and density calculations of trait space require n+1 species, where n is the number of dimensions in morphospace (n=8)) (Appendix S1, Figures S1, S3). One species, Narcondam hornbill (*Aceros narcondami)*, is only found in a single grid cell with 6 other species, and so *A. narcondami* was omitted from our dataset. Further, we removed helmeted curassow (*Pauxi pauxi)* from analysis due to its unusual, and extreme bill ornamentation. Its bill knob is developmentally part of the beak and so included in defining its shape, whereas in other species including cassowaries this is not the case, thus *P. pauxi* fills an extreme area of morphospace and inflates diversity scores based on traits for cells it occurs in.

c) Defining Phyloregions

We defined phyloregions using a similar protocol to Holt et al. (2013). Specifically, we first calculated phylogenetic beta diversity for the spatial presence absence matrix using the phylosor.query function in the R package PhyloMeasures (Tsirogiannis and Brody, 2017). We then clustered the resulting matrix using the upgma function in the phangorn package (Schliep, 2011). We then applied a "time slice" to the clustered tree using the treeSlice function in the phytools package (Revell, 2012) to define an initial set of phyloregions. The time slice was set at 90% of the root to tip distance of the UPGMA tree. This resulted in 13

phyloregions containing a minimum of 50 grid cells. We note that the cut-off for this slicing is arbitrary (see Holt et al., 2013 and Kreft & Jetz 2010). We found that the 90% yielded regions that were coherent and largely comparable to previous studies. In addition, we emphasise that our aim was to produce functional units for the delimitation of source pools for null models, rather than to propose new zoogeographic regions. Some grid cells fell outside the clusters. Cells that were sister to one of the 13 regions were assigned to their neighbouring cluster. 99 cells that split at the root of the tree could not be unambiguously assigned to any cluster and were omitted from subsequent phyloregion analysis.

d) Environmental Correlates

We used a 2019 dataset of global habitat types from the Copernicus Land Monitoring Service (Buchhorn *et al.* 2020) to quantify the main habitat type and diversity of habitat types in each 100 km grid cell. The modal habitat type from 19 habitat classifications was calculated for each 1 km grid cell under Behrmann projection. We then calculated the aggregated modal habitat type, and Shannon's index (as a score of habitat heterogeneity) for each 100 km grid cell. Altitudinal data at a 30 arc-second resolution was accessed via the WorldClim database (Fick & Hijmans 2017) using the *getData* function in the R package *raster* (version 3.3.13: Hijmans, 2020). This data was re-projected to a Behrmann projection, and the average altitude calculated at a 1 km grid cell resolution. For each 100 km grid cell, the altitudinal range was then calculated from the minimum and maximum altitudes of the 1 km grid cells contained within. An average score of global gross primary productivity (GPP) was calculated for each 100 km grid cell using annual data across the years 2000 – 2016 (Zhang *et al.* 2017b, a). For each year, GPP data was transferred to a Behrman projection at 1km resolution, and

then the average GPP value calculated for each 100 km grid cell. The mean value of GPP across years was then calculated.

Figure S1: The proportion of species in each bird family represented in our dataset. Light yellow indicates no species are missing from that family. The darker the colour, the more species are missing trait data and/or range data. The number of species present, and the total number of species in each family are given next to each family name in the phylogeny. Phylogeny plotted using the *ggtree* package (Yu *et al.* 2017) in R Studio (RStudio Team 2020).

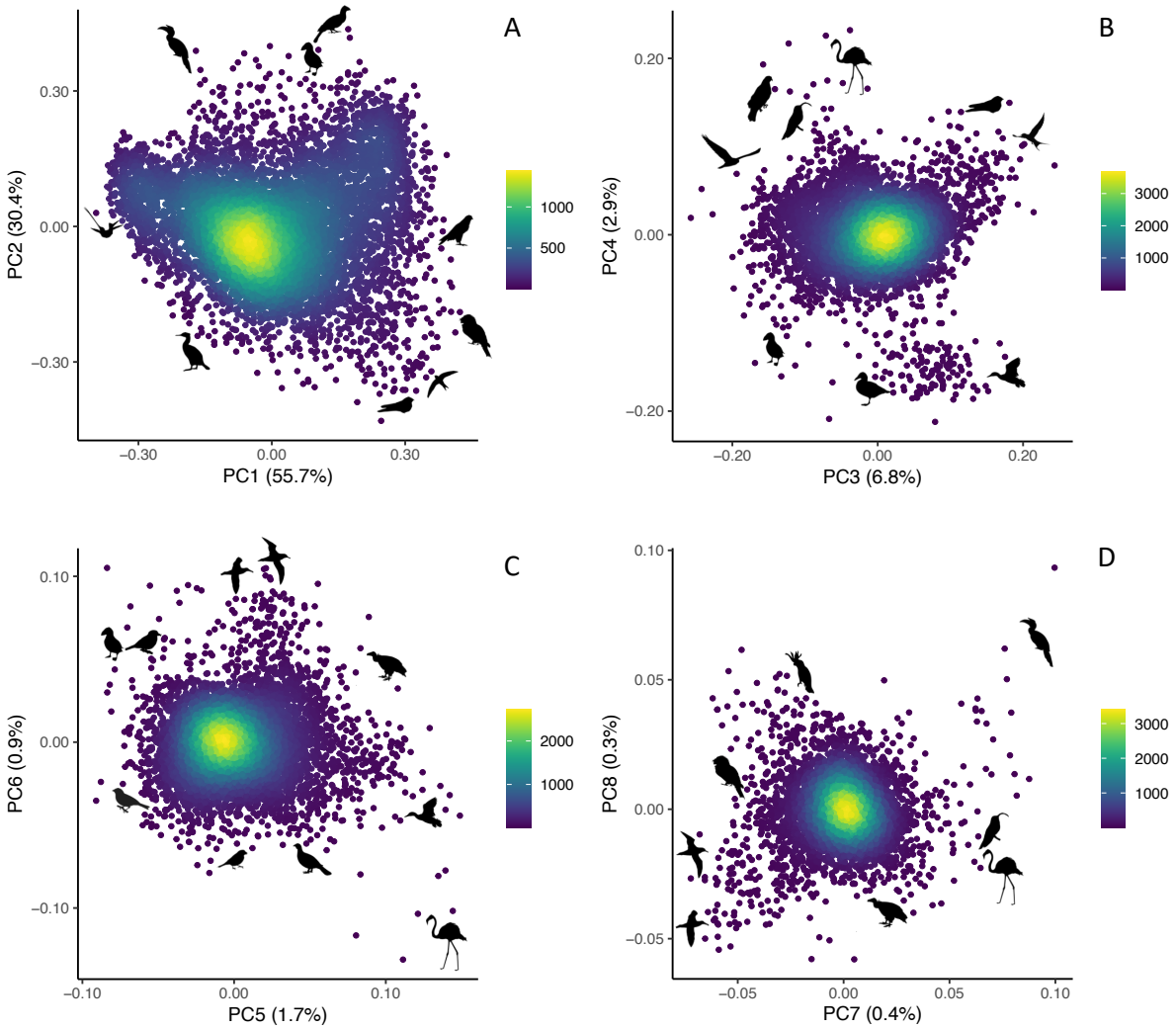

Figure S2: Scatterplots showing the first 8 principal components of beak shape, and the proportion of variance represented by each. The scale bar shows the number of neighbouring points within one standard deviation of the Euclidean distance of each species to all other species across both axes for each scatterplot. Points were coloured with yellow being where species are most numerous, and purple least numerous. All silhouettes are in the public domain and were downloaded from PhyloPic.org. Over 98% of beak shape variation is captured by the first 7 principal components, with the first principal components representing over half (55.7%) of this variation. PC8 is presented here as a means to plot against PC7 but is not used in analysis. Beak PC1 describes the relationship between bill length, width, and depth, varying from extremely long, slender bills, such as the sword-billed hummingbird (*Ensifera ensifera*) to short, wide beaks like that of frogmouths (Podargidae). The remaining 44.3% of total variation in beak shape is captured by more complex aspects of beak shape, with some groups of species showing particularly extreme PC values on one (e.g., waterfowl [Anseriformes], PC4) or many axes (e.g., flamingos [Phoenicopteriformes], PCs 4,5,6), strongly deviating from variations on a cone shape.

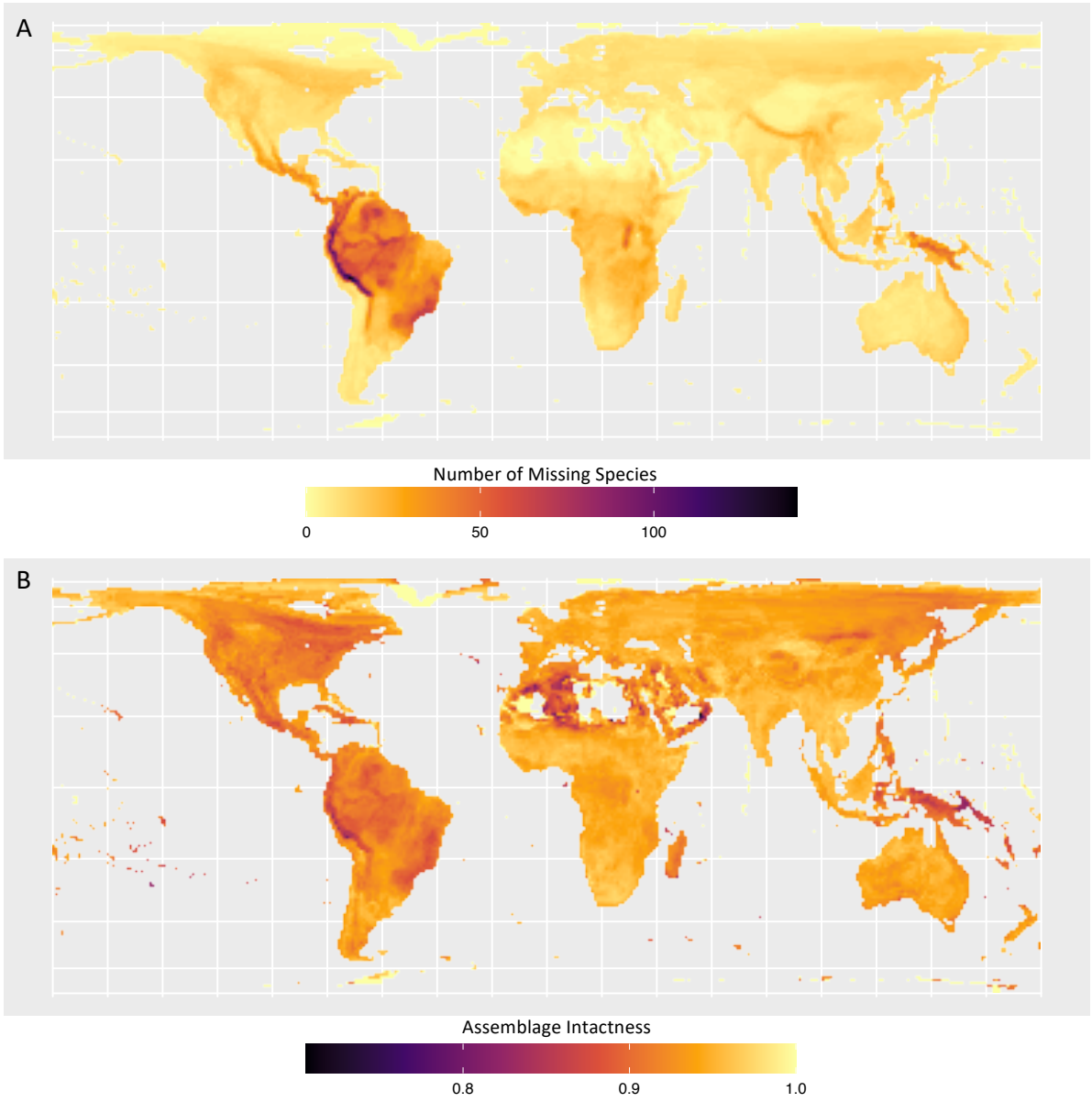

Figure S3: A) The number of species with missing trait data in each grid cell. Light yellow indicates 0 species missing. The darker the colour, the more species are missing trait data (to a max of 141, and median of 10 species missing). B) The intactness of each assemblage (i.e., grid cell), once species without trait data have been removed. 1.0, light yellow, is a completely intact community. The least intact community contains 70.59% of species, and the median value is 94.03%.

Table S1: Proportion of variance represented by each component from principal components analyses of A) beak shape, and B) scaled morphological trait data. 11 PCs are presented out of 129 PCs for A) beak shape.

Input Trait Matrix	**Importance of PCs**	**PC 1**	**PC 2**	**PC 3**	**PC 4**	**PC 5**	**PC 6**	**PC 7**	**PC 8**	**PC 9**	**PC 10**	**PC 11**
A) Beak Shape Matrix	Proportion of Variance	0.557	0.304	0.068	0.029	0.017	0.009	0.004	0.003	0.002	0.001	0.001
	Cumulative Proportion	0.557	0.860	0.929	0.958	0.975	0.984	0.989	0.992	0.994	0.995	0.996
B) Scaled Trait Matrix	Proportion of Variance	0.351	0.100	0.093	0.091	0.091	0.091	0.091	0.054	0.025	0.010	0.004
	Cumulative Proportion	0.351	0.451	0.544	0.635	0.726	0.817	0.908	0.961	0.986	0.996	1.000

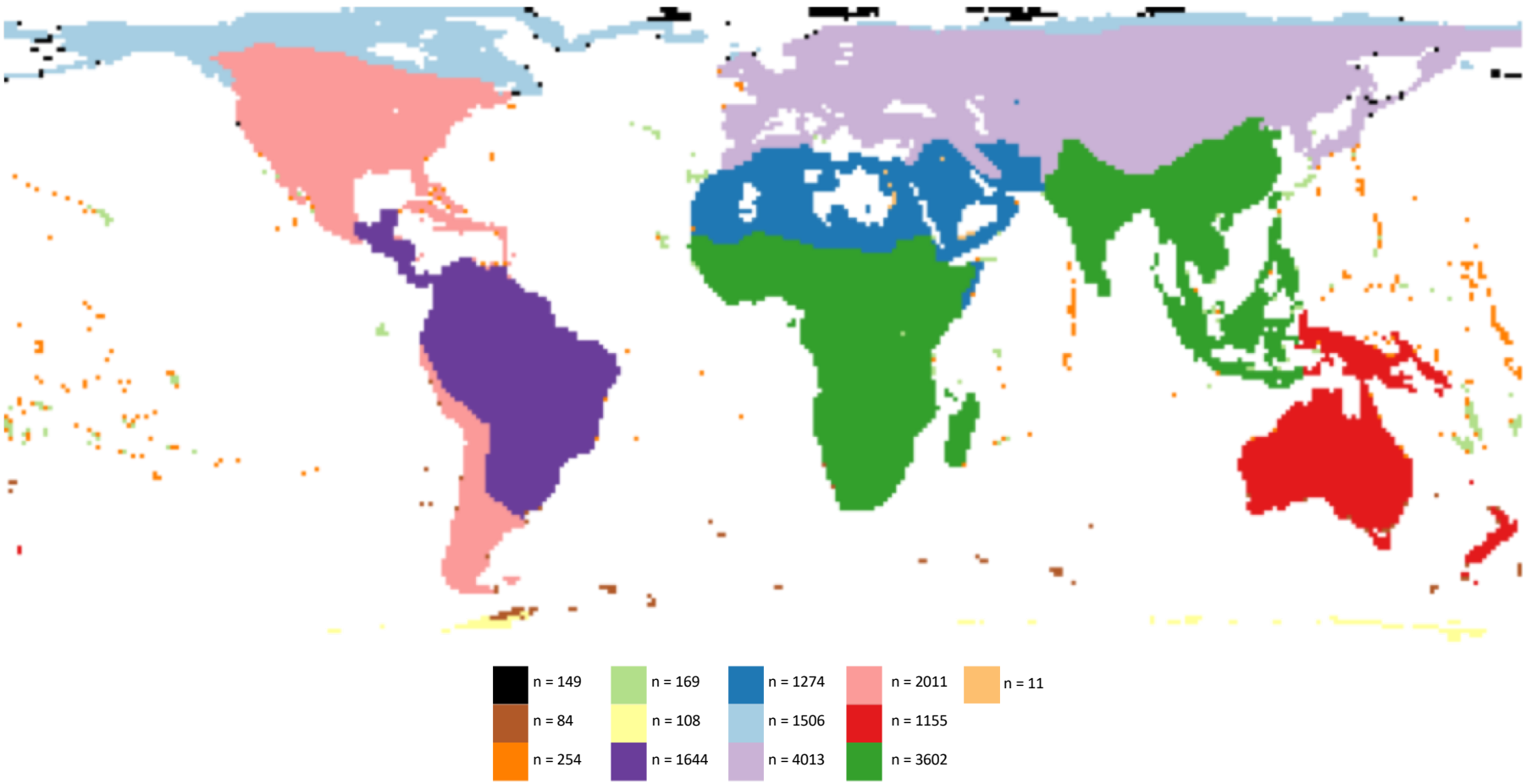

Figure S4: Phylogenetically distinct phyloregions were used to define species pools to avoid sampling from historically different assemblages. We define 13 unique phyloregions shown in different colours. n denotes the number of 100km^2 grid cells present in each phyloregion.

Table S2: AIC values for all models tested with morphological variance (sum of variances) SES and morphological density (mean nearest neighbour distance) SES as dependent variables. Predictor variables were either all included (species richness, assemblage ED (sum of equal splits) SES, gross primary productivity (GPP), habitat heterogeneity (Shannon's index), altitudinal range and main land type), all included apart from land type, or land type only. To account for spatial autocorrelation a variety of correlation structures were included in the models. The most well supported models with the lowest AIC scores for each dependent variable are highlighted in bold. Models were run and tested on 25% subsets of the complete dataset (n=15277), dataset A, B, C and D.

Dataset	Dependent Variable (Species Pool)	Predictor Variables	Correlation Structure	Nugget	AIC
A	Variance SES (Global)	All	None	True	14166.785
A	Variance SES (Global)	All	Exponential	True	8353.757
A	Variance SES (Global)	All	Exponential	False	8351.949
A	Variance SES (Global)	All	Gaussian	True	8787.835
A	Variance SES (Global)	All	Spherical	True	8358.329
A	Variance SES (Global)	All (minus land type)	None	True	14550.117
A	Variance SES (Global)	All (minus land type)	Exponential	True	8297.909
A	**Variance SES (Global)**	**All (minus land type)**	**Exponential**	**False**	**8296.148**
A	Variance SES (Global)	All (minus land type)	Gaussian	True	8736.066
A	Variance SES (Global)	All (minus land type)	Spherical	True	8302.893
A	Variance SES (Global)	Land type only	None	True	14887.646
A	Variance SES (Global)	Land type only	Exponential	True	8828.984
A	Variance SES (Global)	Land type only	Exponential	False	8826.984
A	Variance SES (Global)	Land type only	Gaussian	True	9298.636
A	Variance SES (Global)	Land type only	Spherical	True	8840.278
B	Variance SES (Global)	All	None	True	14134.967
B	Variance SES (Global)	All	Exponential	True	8438.229
B	Variance SES (Global)	All	Exponential	False	8438.507
B	Variance SES (Global)	All	Gaussian	True	9974.707
B	Variance SES (Global)	All	Spherical	True	8438.077
B	Variance SES (Global)	All (minus land type)	None	True	14506.969

B	**Variance SES (Global)**	**All (minus land type)**	**Exponential**	**True**	**8390.070**
B	Variance SES (Global)	All (minus land type)	Exponential	False	8390.247
B	Variance SES (Global)	All (minus land type)	Gaussian	True	8828.203
B	Variance SES (Global)	All (minus land type)	Spherical	True	8390.213
B	Variance SES (Global)	Land type only	None	True	14887.941
B	Variance SES (Global)	Land type only	Exponential	True	9060.907
B	Variance SES (Global)	Land type only	Exponential	False	9059.498
B	Variance SES (Global)	Land type only	Gaussian	True	9500.794
B	Variance SES (Global)	Land type only	Spherical	True	9068.189
C	Variance SES (Global)	All	None	True	14141.351
C	Variance SES (Global)	All	Exponential	True	8448.062
C	Variance SES (Global)	All	Exponential	False	8446.062
C	Variance SES (Global)	All	Gaussian	True	8941.326
C	Variance SES (Global)	All	Spherical	True	8454.492
C	Variance SES (Global)	All (minus land type)	None	True	14597.979
C	Variance SES (Global)	All (minus land type)	Exponential	True	8385.569
C	**Variance SES (Global)**	**All (minus land type)**	**Exponential**	**False**	**8383.569**
C	Variance SES (Global)	All (minus land type)	Gaussian	True	8887.835
C	Variance SES (Global)	All (minus land type)	Spherical	True	8392.075
C	Variance SES (Global)	Land type only	None	True	14827.882
C	Variance SES (Global)	Land type only	Exponential	True	9031.902
C	Variance SES (Global)	Land type only	Exponential	False	9029.902
C	Variance SES (Global)	Land type only	Gaussian	True	9486.700
C	Variance SES (Global)	Land type only	Spherical	True	9039.728
D	Variance SES (Global)	All	None	True	14075.277
D	Variance SES (Global)	All	Exponential	True	8524.954
D	Variance SES (Global)	All	Exponential	False	8539.732
D	Variance SES (Global)	All	Gaussian	True	8855.373
D	Variance SES (Global)	All	Spherical	True	8529.060
D	Variance SES (Global)	All (minus land type)	None	True	14539.397

D	**Variance SES (Global)**	**All (minus land type)**	**Exponential**	**True**	**8474.811**
D	Variance SES (Global)	All (minus land type)	Exponential	False	8488.564
D	Variance SES (Global)	All (minus land type)	Gaussian	True	8812.950
D	Variance SES (Global)	All (minus land type)	Spherical	True	8476.503
D	Variance SES (Global)	Land type only	None	True	14783.540
D	Variance SES (Global)	Land type only	Exponential	True	9112.595
D	Variance SES (Global)	Land type only	Exponential	False	9115.883
D	Variance SES (Global)	Land type only	Gaussian	True	9447.835
D	Variance SES (Global)	Land type only	Spherical	True	9132.561
A	Variance SES (Phyloregion)	All	None	True	14227.516
A	Variance SES (Phyloregion)	All	Exponential	True	8764.052
A	Variance SES (Phyloregion)	All	Exponential	False	8762.108
A	Variance SES (Phyloregion)	All	Gaussian	True	9185.381
A	Variance SES (Phyloregion)	All	Spherical	True	8786.198
A	Variance SES (Phyloregion)	All (minus land type)	None	True	14501.877
A	Variance SES (Phyloregion)	All (minus land type)	Exponential	True	8714.153
A	**Variance SES (Phyloregion)**	**All (minus land type)**	**Exponential**	**False**	**8712.255**
A	Variance SES (Phyloregion)	All (minus land type)	Gaussian	True	9137.892
A	Variance SES (Phyloregion)	All (minus land type)	Spherical	True	8736.722
A	Variance SES (Phyloregion)	Land type only	None	True	15912.587
A	Variance SES (Phyloregion)	Land type only	Exponential	True	9209.669
A	Variance SES (Phyloregion)	Land type only	Exponential	False	9207.669
A	Variance SES (Phyloregion)	Land type only	Gaussian	True	9706.252
A	Variance SES (Phyloregion)	Land type only	Spherical	True	9218.216
B	Variance SES (Phyloregion)	All	None	True	14167.899
B	Variance SES (Phyloregion)	All	Exponential	True	8894.297
B	Variance SES (Phyloregion)	All	Exponential	False	8899.843
B	Variance SES (Phyloregion)	All	Gaussian	True	9276.581
B	Variance SES (Phyloregion)	All	Spherical	True	8899.372
B	Variance SES (Phyloregion)	All (minus land type)	None	True	14398.324

B	**Variance SES (Phyloregion)**	**All (minus land type)**	**Exponential**	**True**	**8856.404**
B	Variance SES (Phyloregion)	All (minus land type)	Exponential	False	8861.505
B	Variance SES (Phyloregion)	All (minus land type)	Gaussian	True	9239.486
B	Variance SES (Phyloregion)	All (minus land type)	Spherical	True	8856.626
B	Variance SES (Phyloregion)	Land type only	None	True	15914.831
B	Variance SES (Phyloregion)	Land type only	Exponential	True	9450.883
B	Variance SES (Phyloregion)	Land type only	Exponential	False	9452.845
B	Variance SES (Phyloregion)	Land type only	Gaussian	True	9897.319
B	Variance SES (Phyloregion)	Land type only	Spherical	True	9458.957
C	Variance SES (Phyloregion)	All	None	True	14185.464
C	Variance SES (Phyloregion)	All	Exponential	True	8901.408
C	Variance SES (Phyloregion)	All	Exponential	False	8899.430
C	Variance SES (Phyloregion)	All	Gaussian	True	9345.019
C	Variance SES (Phyloregion)	All	Spherical	True	8906.246
C	Variance SES (Phyloregion)	All (minus land type)	None	True	14490.098
C	Variance SES (Phyloregion)	All (minus land type)	Exponential	True	8851.028
C	**Variance SES (Phyloregion)**	**All (minus land type)**	**Exponential**	**False**	**8849.028**
C	Variance SES (Phyloregion)	All (minus land type)	Gaussian	True	9298.486
C	Variance SES (Phyloregion)	All (minus land type)	Spherical	True	8858.345
C	Variance SES (Phyloregion)	Land type only	None	True	15859.762
C	Variance SES (Phyloregion)	Land type only	Exponential	True	9396.866
C	Variance SES (Phyloregion)	Land type only	Exponential	False	9394.866
C	Variance SES (Phyloregion)	Land type only	Gaussian	True	9884.858
C	Variance SES (Phyloregion)	Land type only	Spherical	True	9405.701
D	Variance SES (Phyloregion)	All	None	True	14034.959
D	Variance SES (Phyloregion)	All	Exponential	True	9051.144
D	Variance SES (Phyloregion)	All	Exponential	False	9072.233
D	Variance SES (Phyloregion)	All	Gaussian	True	9350.550
D	Variance SES (Phyloregion)	All	Spherical	True	9058.903
D	Variance SES (Phyloregion)	All (minus land type)	None	True	14392.547

D	**Variance SES (Phyloregion)**	**All (minus land type)**	**Exponential**	**True**	**9008.977**
D	Variance SES (Phyloregion)	All (minus land type)	Exponential	False	9027.841
D	Variance SES (Phyloregion)	All (minus land type)	Gaussian	True	9314.491
D	Variance SES (Phyloregion)	All (minus land type)	Spherical	True	9012.831
D	Variance SES (Phyloregion)	Land type only	None	True	15876.186
D	Variance SES (Phyloregion)	Land type only	Exponential	True	9583.433
D	Variance SES (Phyloregion)	Land type only	Exponential	False	9593.660
D	Variance SES (Phyloregion)	Land type only	Gaussian	True	9940.135
D	Variance SES (Phyloregion)	Land type only	Spherical	True	NA
A	Density SES (Global)	All	None	True	11447.308
A	Density SES (Global)	All	Exponential	True	6786.332
A	Density SES (Global)	All	Exponential	False	6824.790
A	Density SES (Global)	All	Gaussian	True	7105.662
A	Density SES (Global)	All	Spherical	True	6797.851
A	Density SES (Global)	All (minus land type)	None	True	11637.312
A	**Density SES (Global)**	**All (minus land type)**	**Exponential**	**True**	**6727.316**
A	Density SES (Global)	All (minus land type)	Exponential	False	6766.402
A	Density SES (Global)	All (minus land type)	Gaussian	True	7051.323
A	Density SES (Global)	All (minus land type)	Spherical	True	6738.328
A	Density SES (Global)	Land type only	None	True	12230.597
A	Density SES (Global)	Land type only	Exponential	True	7364.345
A	Density SES (Global)	Land type only	Exponential	False	7370.690
A	Density SES (Global)	Land type only	Gaussian	True	7697.721
A	Density SES (Global)	Land type only	Spherical	True	7397.104
B	Density SES (Global)	All	None	True	11463.155
B	Density SES (Global)	All	Exponential	True	6647.496
B	Density SES (Global)	All	Exponential	False	6681.249
B	Density SES (Global)	All	Gaussian	True	6966.920
B	Density SES (Global)	All	Spherical	True	6664.004
B	Density SES (Global)	All (minus land type)	None	True	11646.051

B	**Density SES (Global)**	**All (minus land type)**	**Exponential**	**True**	**6587.660**
B	Density SES (Global)	All (minus land type)	Exponential	False	6619.693
B	Density SES (Global)	All (minus land type)	Gaussian	True	6910.042
B	Density SES (Global)	All (minus land type)	Spherical	True	6602.764
B	Density SES (Global)	Land type only	None	True	12222.247
B	Density SES (Global)	Land type only	Exponential	True	7314.773
B	Density SES (Global)	Land type only	Exponential	False	7321.717
B	Density SES (Global)	Land type only	Gaussian	True	7681.601
B	Density SES (Global)	Land type only	Spherical	True	7362.321
C	Density SES (Global)	All	None	True	11334.912
C	Density SES (Global)	All	Exponential	True	6578.856
C	Density SES (Global)	All	Exponential	False	6589.797
C	Density SES (Global)	All	Gaussian	True	6965.280
C	Density SES (Global)	All	Spherical	True	6608.045
C	Density SES (Global)	All (minus land type)	None	True	11536.559
C	**Density SES (Global)**	**All (minus land type)**	**Exponential**	**True**	**6530.123**
C	Density SES (Global)	All (minus land type)	Exponential	False	6540.535
C	Density SES (Global)	All (minus land type)	Gaussian	True	6925.668
C	Density SES (Global)	All (minus land type)	Spherical	True	6559.882
C	Density SES (Global)	Land type only	None	True	12095.721
C	Density SES (Global)	Land type only	Exponential	True	7196.423
C	Density SES (Global)	Land type only	Exponential	False	7195.900
C	Density SES (Global)	Land type only	Gaussian	True	7590.859
C	Density SES (Global)	Land type only	Spherical	True	7246.254
D	Density SES (Global)	All	None	True	11500.909
D	Density SES (Global)	All	Exponential	True	6696.152
D	Density SES (Global)	All	Exponential	False	6711.444
D	Density SES (Global)	All	Gaussian	True	7077.771
D	Density SES (Global)	All	Spherical	True	6703.722
D	Density SES (Global)	All (minus land type)	None	True	11729.588

D	**Density SES (Global)**	**All (minus land type)**	**Exponential**	**True**	**6655.342**
D	Density SES (Global)	All (minus land type)	Exponential	False	6669.339
D	Density SES (Global)	All (minus land type)	Gaussian	True	7043.989
D	Density SES (Global)	All (minus land type)	Spherical	True	6668.813
D	Density SES (Global)	Land type only	None	True	12295.712
D	Density SES (Global)	Land type only	Exponential	True	7393.515
D	Density SES (Global)	Land type only	Exponential	False	7392.522
D	Density SES (Global)	Land type only	Gaussian	True	7786.394
D	Density SES (Global)	Land type only	Spherical	True	7450.550
A	Density SES (Phyloregion)	All	None	True	11376.183
A	Density SES (Phyloregion)	All	Exponential	True	6904.891
A	Density SES (Phyloregion)	All	Exponential	False	6935.544
A	Density SES (Phyloregion)	All	Gaussian	True	7202.917
A	Density SES (Phyloregion)	All	Spherical	True	6916.066
A	Density SES (Phyloregion)	All (minus land type)	None	True	11510.065
A	**Density SES (Phyloregion)**	**All (minus land type)**	**Exponential**	**True**	**6841.262**
A	Density SES (Phyloregion)	All (minus land type)	Exponential	False	6871.832
A	Density SES (Phyloregion)	All (minus land type)	Gaussian	True	7143.631
A	Density SES (Phyloregion)	All (minus land type)	Spherical	True	6853.944
A	Density SES (Phyloregion)	Land type only	None	True	13694.872
A	Density SES (Phyloregion)	Land type only	Exponential	True	7120.468
A	Density SES (Phyloregion)	Land type only	Exponential	False	7157.571
A	Density SES (Phyloregion)	Land type only	Gaussian	True	7554.606
A	Density SES (Phyloregion)	Land type only	Spherical	True	7134.618
B	Density SES (Phyloregion)	All	None	True	11351.960
B	Density SES (Phyloregion)	All	Exponential	True	6819.062
B	Density SES (Phyloregion)	All	Exponential	False	6844.247
B	Density SES (Phyloregion)	All	Gaussian	True	7124.879
B	Density SES (Phyloregion)	All	Spherical	True	6829.840
B	Density SES (Phyloregion)	All (minus land type)	None	True	11489.173

B	**Density SES (Phyloregion)**	**All (minus land type)**	**Exponential**	**True**	**6759.021**
B	Density SES (Phyloregion)	All (minus land type)	Exponential	False	6782.620
B	Density SES (Phyloregion)	All (minus land type)	Gaussian	True	7068.905
B	Density SES (Phyloregion)	All (minus land type)	Spherical	True	6777.159
B	Density SES (Phyloregion)	Land type only	None	True	13747.758
B	Density SES (Phyloregion)	Land type only	Exponential	True	7144.154
B	Density SES (Phyloregion)	Land type only	Exponential	False	7174.153
B	Density SES (Phyloregion)	Land type only	Gaussian	True	7586.496
B	Density SES (Phyloregion)	Land type only	Spherical	True	7155.479
C	Density SES (Phyloregion)	All	None	True	11268.102
C	Density SES (Phyloregion)	All	Exponential	True	6658.943
C	Density SES (Phyloregion)	All	Exponential	False	6664.774
C	Density SES (Phyloregion)	All	Gaussian	True	7024.092
C	Density SES (Phyloregion)	All	Spherical	True	6683.438
C	Density SES (Phyloregion)	All (minus land type)	None	True	11417.549
C	**Density SES (Phyloregion)**	**All (minus land type)**	**Exponential**	**True**	**6608.405**
C	Density SES (Phyloregion)	All (minus land type)	Exponential	False	6613.772
C	Density SES (Phyloregion)	All (minus land type)	Gaussian	True	6986.045
C	Density SES (Phyloregion)	All (minus land type)	Spherical	True	6631.229
C	Density SES (Phyloregion)	Land type only	None	True	13624.329
C	Density SES (Phyloregion)	Land type only	Exponential	True	6884.108
C	Density SES (Phyloregion)	Land type only	Exponential	False	6889.465
C	Density SES (Phyloregion)	Land type only	Gaussian	True	7395.183
C	Density SES (Phyloregion)	Land type only	Spherical	True	6909.025
D	Density SES (Phyloregion)	All	None	True	11360.997
D	Density SES (Phyloregion)	All	Exponential	True	6834.842
D	Density SES (Phyloregion)	All	Exponential	False	6853.366
D	Density SES (Phyloregion)	All	Gaussian	True	7180.666
D	Density SES (Phyloregion)	All	Spherical	True	6846.661
D	Density SES (Phyloregion)	All (minus land type)	None	True	11538.593

D	**Density SES (Phyloregion)**	**All (minus land type)**	**Exponential**	**True**	**6781.013**
D	Density SES (Phyloregion)	All (minus land type)	Exponential	False	6798.445
D	Density SES (Phyloregion)	All (minus land type)	Gaussian	True	7133.893
D	Density SES (Phyloregion)	All (minus land type)	Spherical	True	6793.222
D	Density SES (Phyloregion)	Land type only	None	True	13776.170
D	Density SES (Phyloregion)	Land type only	Exponential	True	7140.684
D	Density SES (Phyloregion)	Land type only	Exponential	False	7158.505
D	Density SES (Phyloregion)	Land type only	Gaussian	True	7603.403
D	Density SES (Phyloregion)	Land type only	Spherical	True	7162.305

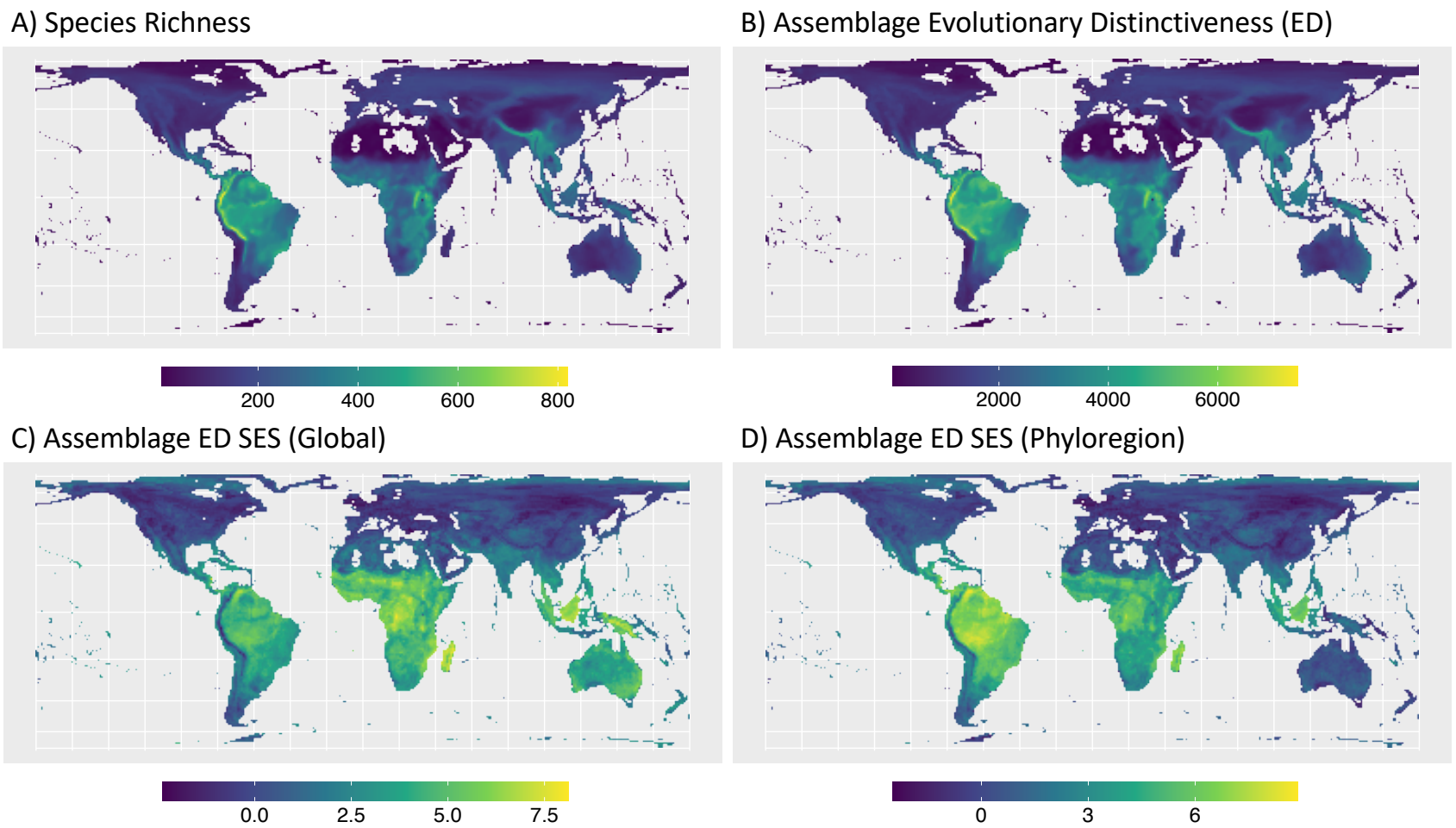

Figure S5: A) Species richness and B) assemblage evolutionary distinctiveness (sum of equal splits) for 8352 bird species across 15980 terrestrial 1 degree grid cells under Behrmann projection. Standard effect sizes (SES) for assemblage ED were calculated from global (**C**) and phyloregional (**D**) species pools.

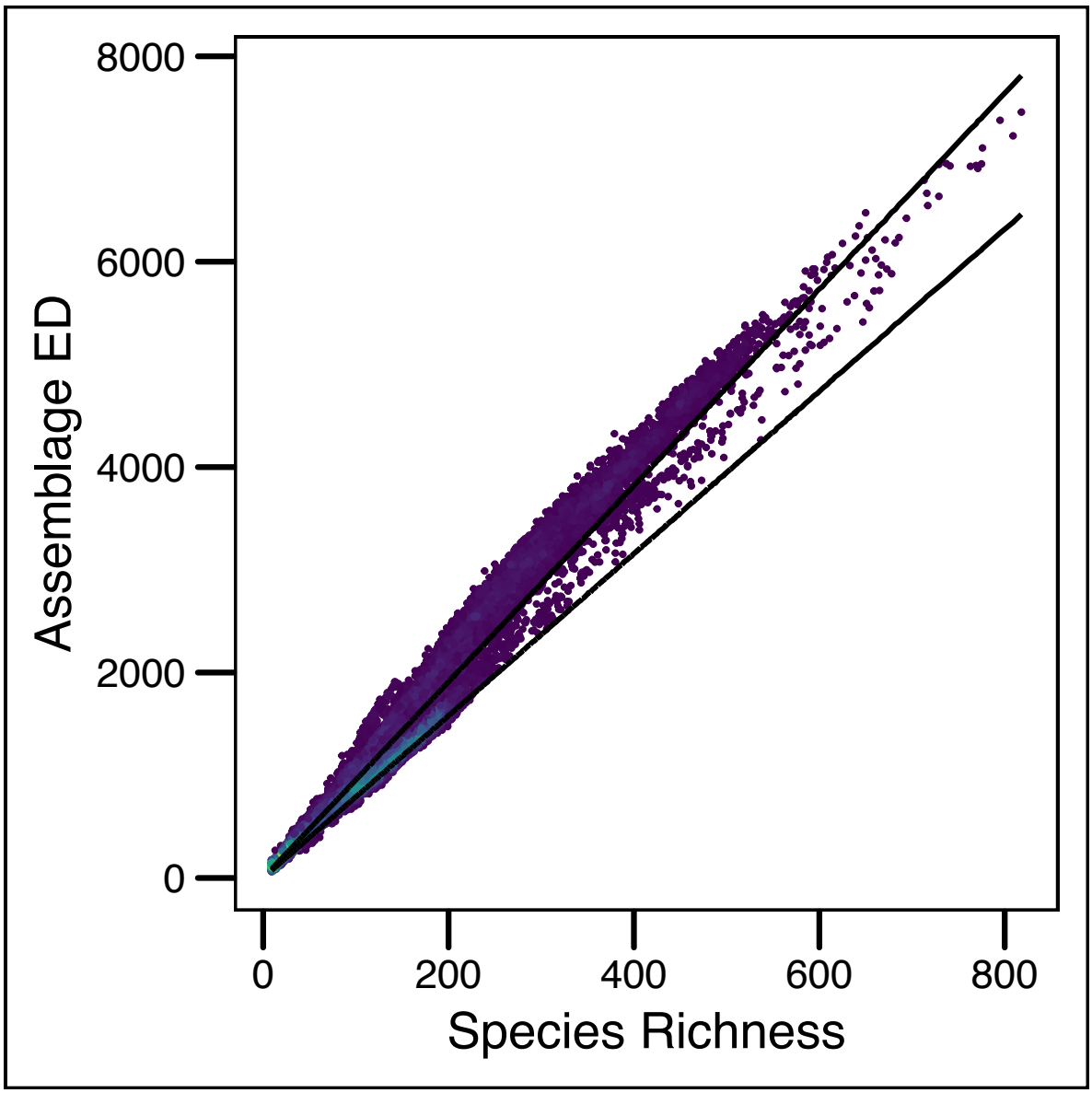

Figure S6: Scatter plot showing the relationship between species richness and assemblage evolutionary distinctiveness (sum of equal splits) Points are coloured according to the number of neighbouring points present to highlight density (Kremer 2019), with yellow the most and purple the least dense. The lines show the upper (97.5) and lower (2.5) quantiles calculated across null communities drawn from a global species pool for each value of species richness.

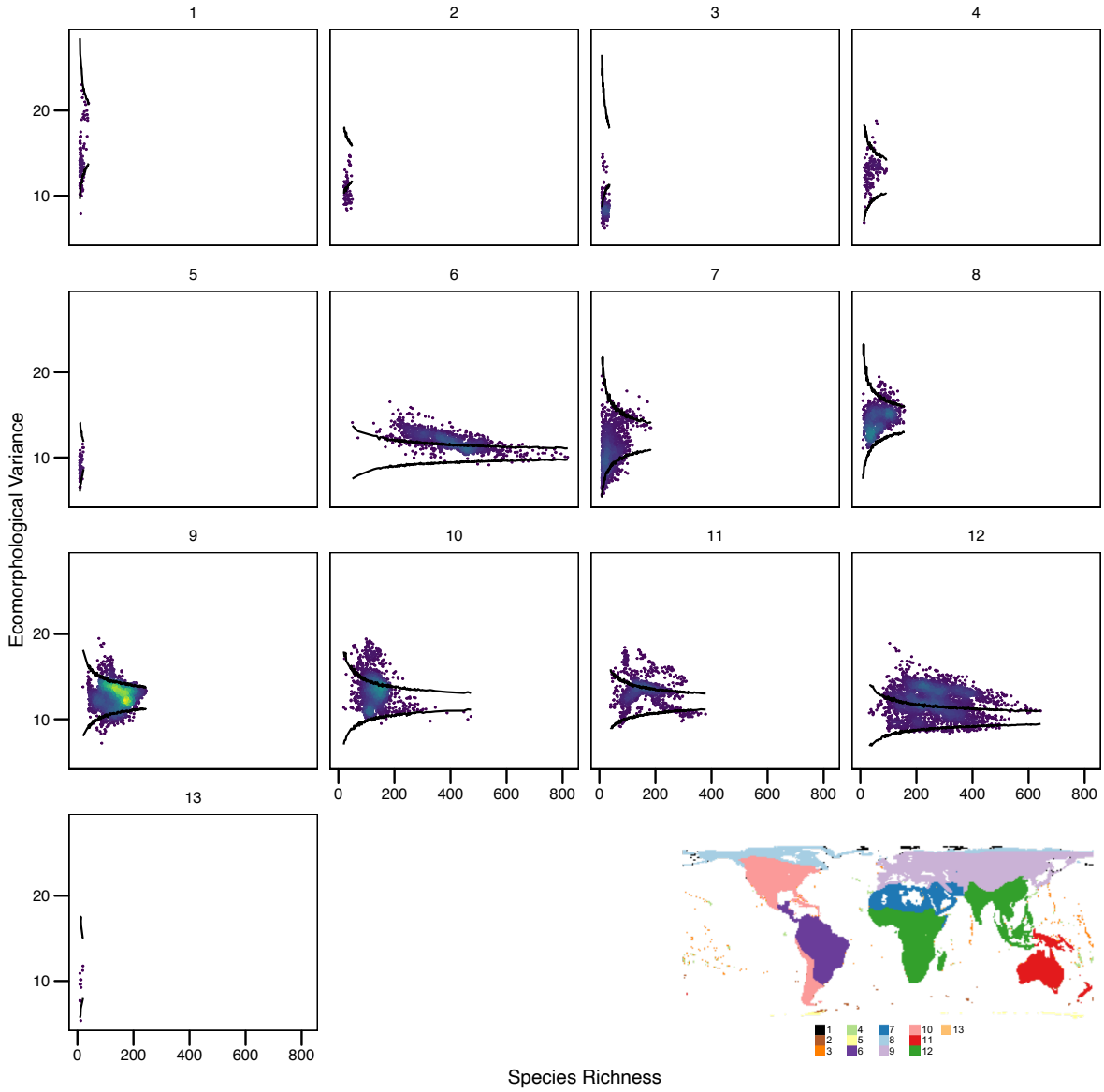

Figure S7: Scatter plots showing the relationship between species richness and morphological variance (sum of variances) in each phyloregion. The ggpointdensity R package (Kremer 2019) was used to colour points according to the number of neighbouring points present to highlight density, with yellow being most dense, and purple being least dense. The lines show the upper (97.5) and lower (2.5) quantiles calculated across null communities drawn from phyloregional species pools for each value of species richness. Inset map shows the different phyloregions.

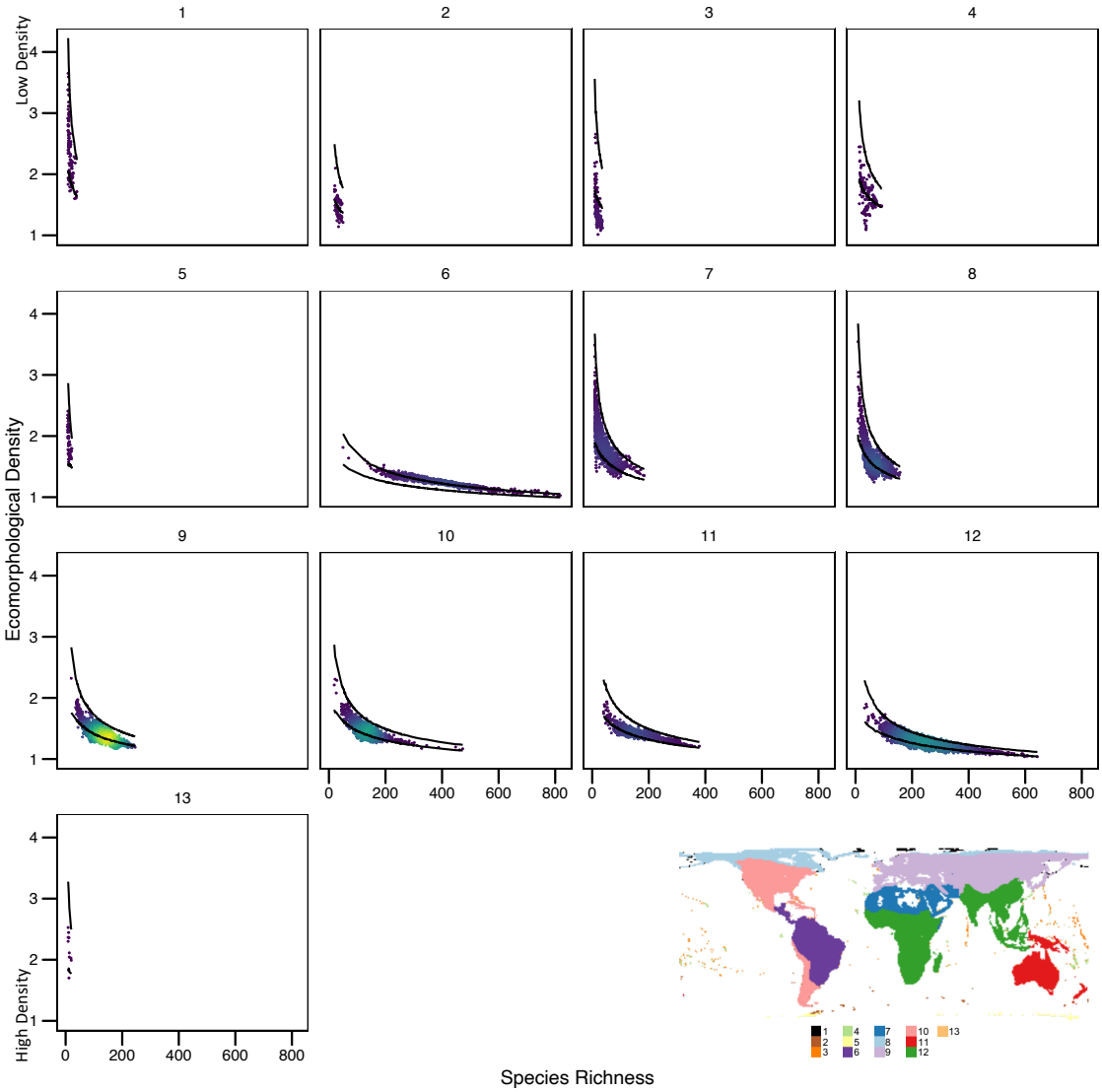

Figure S8: Scatter plots showing the relationship between species richness and morphological density (mean nearest neighbor distance) in each phyloregion. The ggpointdensity R package (Kremer 2019) was used to colour points according to the number of neighbouring points present to highlight density, with yellow being most dense, and purple being least dense. The lines show the upper (97.5) and lower (2.5) quantiles calculated across null communities drawn from phyloregional species pools for each value of species richness. Inset map shows the different phyloregions.

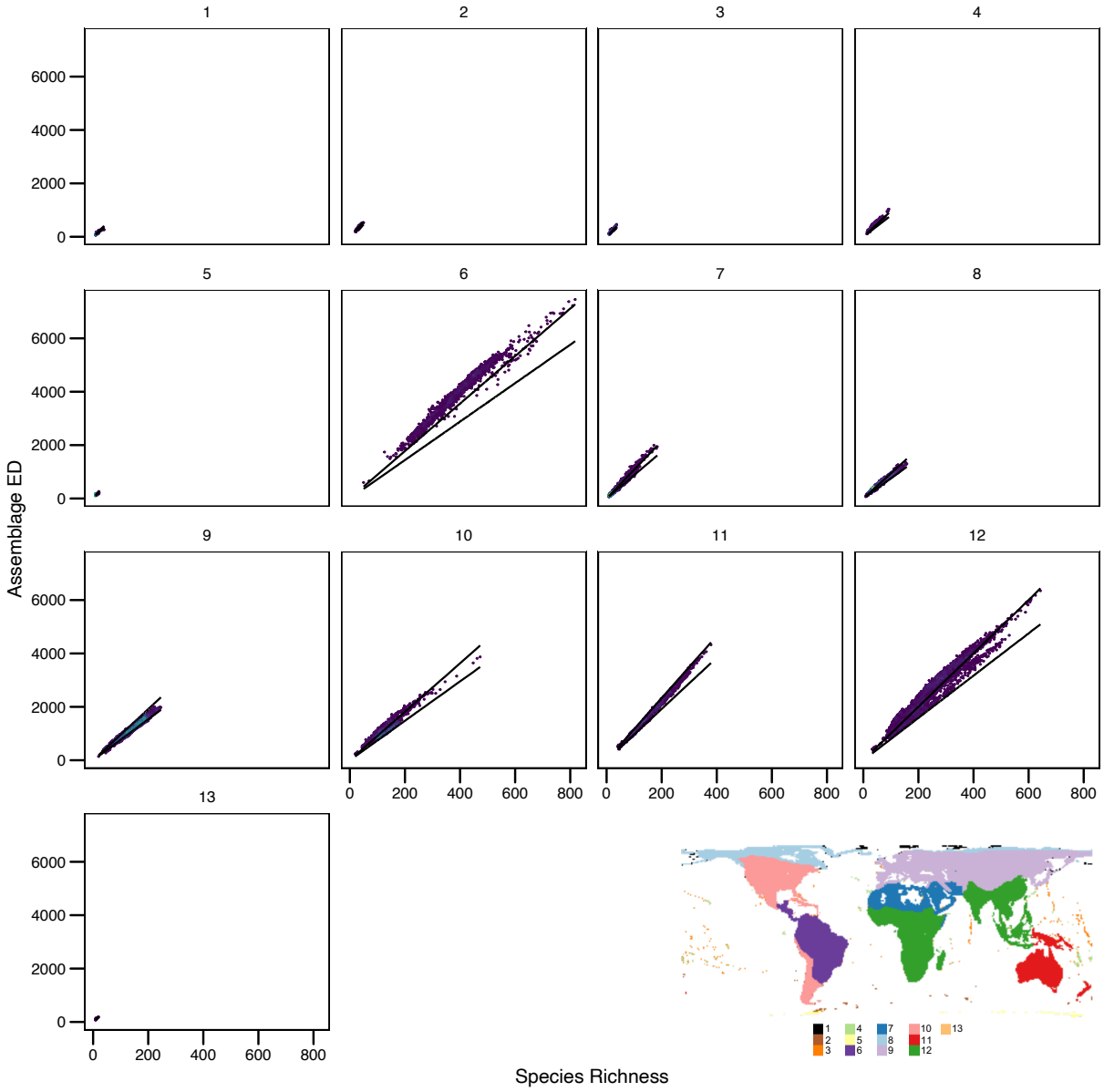

Figure S9: Scatter plots showing the relationship between species richness and assemblage ED (sum of equal splits) in each phyloregion. The ggpointdensity R package (Kremer 2019) was used to colour points according to the number of neighbouring points present to highlight density, with yellow being most dense, and purple being least dense. The lines show the upper (97.5) and lower (2.5) quantiles calculated across null communities drawn from phyloregional species pools for each value of species richness. Inset map shows the different phyloregions.

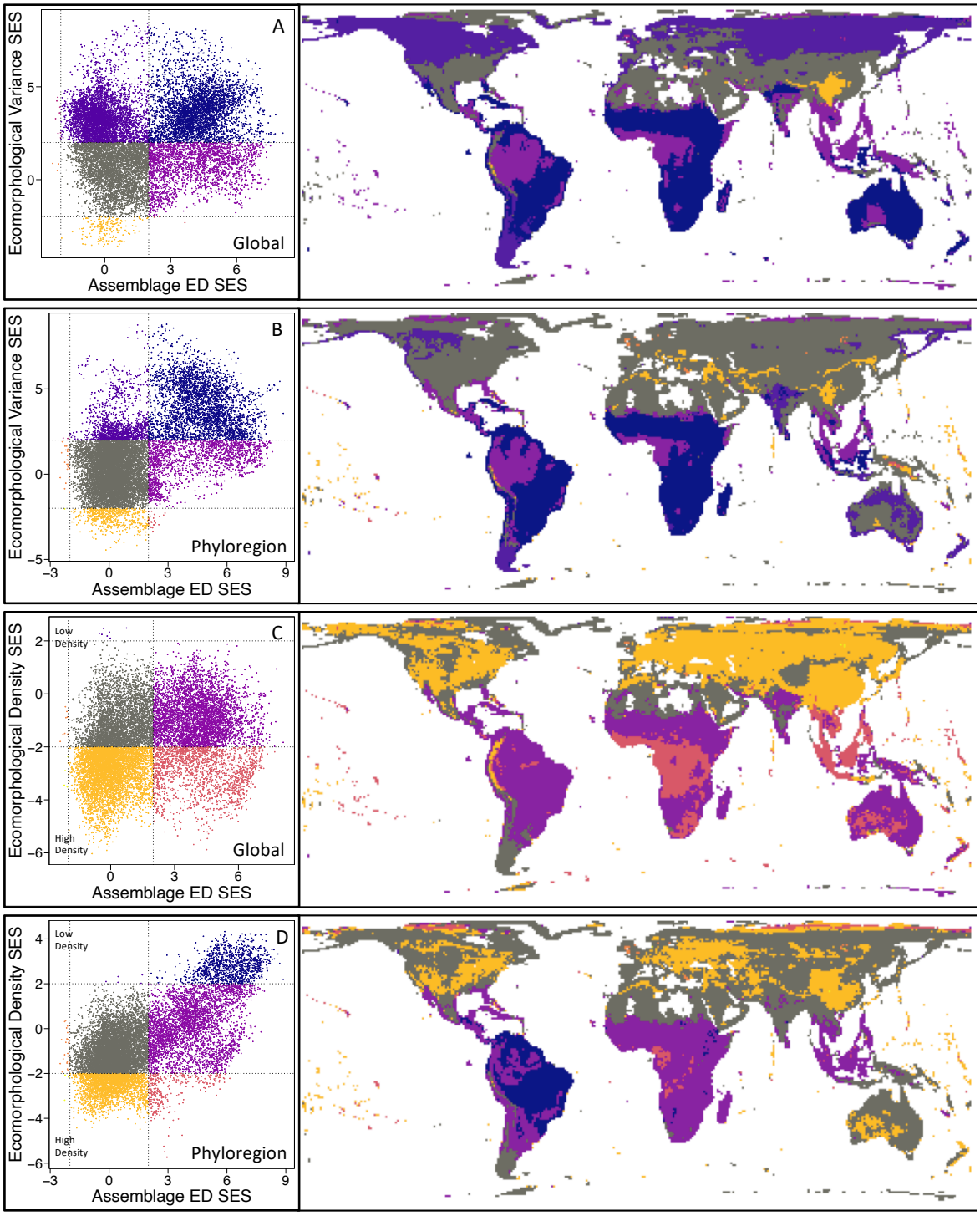

Figure S10: Areas of the globe where the standard effect sizes (SES) of different biodiversity metrics (morphological variance (sum of variances), morphological density (mean nearest neighbour distance) and assemblage ED (sum of equal splits)) show statistically significant deviation from expected (+/- 2) for 8352 bird species across 15980 terrestrial 1 degree grid cells under Behrmann projection. Combinations of variables are A) morphological variance SES and assemblage ED SES where SES was calculated using global species pools, and B) phyloregional species pools, C) morphological density SES

and assemblage ED SES, where SES was calculated using global species pools, and D) phyloregional species pools. The grey colour shows no significant deviation from expected.

Table S3: Best-fit multi-predictor GLS models of morphological variance (sum of variances) SES and morphological density (mean nearest neighour distance) SES for phyloregional and global species pools. Best-fit models have an exponential spatial autocorrelation structure, and contain all predictors (species richness, assemblage ED (sum of equal splits) SES, gross primary productivity (GPP), habitat heterogeneity (Shannon's index) and altitudinal range), except land type, and had the lowest value for Aikaike's information criterion (AIC). Each 25% subset of data is presented under dataset A, B, C and D. * indicates significance (* p<0.05, ** p<0.01, ***p<0.001). The paramater estimates for each model are given. Species richness, GPP, habitat heterogeneity and altitudinal range were all log-transformed.

	Variance SES (Global)	**Variance SES (Phyloregion)**	**Density SES (Global)**	**Density SES (Phyloregion)**
Predictor	**Parameter estimate (± s.e.)**			
Dataset A				
Species richness	7.577 (±0.556)***	3.574 (±0.587)***	2.961 (±0.447)***	-0.822 (±0.454)
Species richness^2	-1.714 (±0.152)***	-0.622 (±0.160)***	-1.196 (±0.122)***	0.262 (±0.124)*
Assemblage ED SES (Global)	0.093 (±0.028)***	NA	0.048 (±0.023)*	NA
Assemblage ED SES (Global)^2	0.011 (±0.005)*	NA	0.023 (±0.004)***	NA
Assemblage ED SES (Phyloregion)	NA	0.047 (±0.027)	NA	0.055 (±0.021)*
Assemblage ED SES (Phyloregion)^2	NA	0.040 (±0.005)***	NA	0.031 (±0.004)***
GPP	0.158 (±0.113)	-0.037 (±0.120)	-0.306 (±0.093)**	-0.218 (±0.094)*
GPP^2	-0.046 (±0.031)	-0.005 (±0.033)	0.060 (±0.026)*	0.037 (±0.026)
Habitat heterogeneity	-0.026 (±0.395)	0.009 (±0.418)	-0.098 (±0.332)	0.077 (±0.337)
Habitat heterogeneity^2	0.937 (±0.811)	0.554 (±0.856)	0.443 (±0.682)	0.015 (±0.691)
Altitudinal range	0.740 (±0.159)***	0.902 (±0.168)***	0.408 (±0.131)**	0.411 (±0.133)**
Altitudinal range^2	-0.210 (±0.032)***	-0.239 (±0.034)***	-0.103 (±0.027)***	-0.098 (±0.027)***
AIC	**8296.148**	**8712.255**	**6727.316**	**6841.262**

Dataset B				
Species richness	8.145 (±0.550)***	4.323 (±0.583)***	4.963 (±0.428)***	1.175 (±0.439)**
Species richness^2	-1.777 (±0.150)***	-0.715 (±0.159)***	-1.613 (±0.117)***	-0.153 (±0.120)
Assemblage ED SES (Global)	0.203 (±0.029)***	NA	0.092 (±0.023)***	NA
Assemblage ED SES (Global)^2	0.008 (±0.005)	NA	0.026 (±0.004)***	NA
Assemblage ED SES (Phyloregion)	NA	0.105 (±0.028)***	NA	0.080 (±0.021)***
Assemblage ED SES (Phyloregion)^2	NA	0.039 (±0.005)***	NA	0.030 (±0.004)***
GPP	-0.106 (±0.116)	-0.255 (±0.123)*	-0.610 (±0.091)***	-0.444 (±0.094)***
GPP^2	-0.001 (±0.032)	0.018 (±0.034)	0.115 (±0.025)***	0.069 (±0.026)**
Habitat heterogeneity	0.718 (±0.391)	0.536 (±0.418)	-0.249 (±0.317)	-0.367 (±0.323)
Habitat heterogeneity^2	-0.439 (±0.812)	-0.405 (±0.869)	0.540 (±0.659)	0.680 (±0.673)
Altitudinal range	0.911 (±0.150)***	0.948 (±0.160)***	0.686 (±0.120)***	0.625 (±0.123)***
Altitudinal range^2	-0.245 (±0.031)***	-0.259 (±0.033)***	-0.153 (±0.025)***	-0.139 (±0.026)***
AIC	**8390.07**	**8856.404**	**6587.66**	**6759.021**
Dataset C				
Species richness	7.910 (±0.550)***	3.781 (±0.585)***	4.040 (±0.427)***	0.355 (±0.433)
Species richness^2	-1.756 (±0.149)***	-0.602 (±0.159)***	-1.425 (±0.116)***	-0.002 (±0.117)
Assemblage ED SES (Global)	0.167 (±0.029)***	NA	0.089 (±0.023)***	NA
Assemblage ED SES (Global)^2	0.007 (±0.005)	NA	0.022 (±0.004)***	NA
Assemblage ED SES (Phyloregion)	NA	0.075 (±0.028)***	NA	0.095 (±0.021)***
Assemblage ED SES (Phyloregion)^2	NA	0.035 (±0.005)***	NA	0.021 (±0.004)***
GPP	0.029 (±0.111)	-0.090 (±0.118)	-0.386 (±0.088)***	-0.314 (±0.088)***
GPP^2	-0.012 (±0.031)	-0.003 (±0.033)	0.082 (±0.024)***	0.066 (±0.024)**
Habitat heterogeneity	0.362 (±0.404)	0.114 (±0.430)	-0.465 (±0.325)	-0.466 (±0.327)
Habitat heterogeneity^2	0.737 (±0.826)	1.059 (±0.879)	1.073 (±0.665)	1.062 (±0.669)

Altitudinal range	1.213 (±0.175)***	1.265 (±0.187)***	0.624 (±0.139)***	0.608 (±0.141)***
Altitudinal range^2	-0.303 (±0.036)***	-0.327 (±0.038)***	-0.146 (±0.029)***	-0.144 (±0.029)***
AIC	**8383.569**	**8849.028**	**6530.123**	**6608.405**
Dataset D				
Species richness	7.508 (±0.550)***	3.776 (±0.592)***	5.235 (±0.434)***	1.300 (±0.442)**
Species richness^2	-1.716 (±0.151)***	-0.685 (±0.162)***	-1.774 (±0.119)***	-0.288 (±0.121)
Assemblage ED SES (Global)	0.239 (±0.028)***	NA	0.142 (±0.022)***	NA
Assemblage ED SES (Global)^2	-0.002 (±0.05)	NA	0.009 (±0.004)*	NA
Assemblage ED SES (Phyloregion)	NA	0.108 (±0.028)***	NA	0.101 (±0.021)***
Assemblage ED SES (Phyloregion)^2	NA	0.034 (±0.005)***	NA	0.024 (±0.003)***
GPP	-0.009 (±0.119)	-0.214 (±0.128)	-0.484 (±0.094)***	-0.395 (±0.096)***
GPP^2	0.014 (±0.033)	0.066 (±0.035)	0.119 (±0.026)***	0.096 (±0.026)***
Habitat heterogeneity	1.148 (±0.419)**	0.734 (±0.451)	-0.093 (±0.332)	-0.113 (±0.339)
Habitat heterogeneity^2	-1.015 (±0.855)	-0.297 (±0.920)	0.518 (±0.679)	0.474 (±0.692)
Altitudinal range	1.387 (±0.191)***	1.567 (±0.206)***	0.893 (±0.151)***	0.809 (±0.155)***
Altitudinal range^2	-0.337 (±0.039)***	-0.378 (±0.042)***	-0.196 (±0.031)***	-0.180 (±0.031)***
AIC	**8474.811**	**9008.977**	**6655.342**	**6781.013**

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APPENDIX 2

Supplementary materials and methods for Chapter 3:

The homogenisation of avian morphological and phylogenetic diversity under the global extinction crisis.

Section S1: Species that appear in our global dataset but were not categorised automatically as present in any terrestrial biome or ecoregion.

A) Species not categorised automatically due to small ranges and subsequently manually assigned to the correct biomes and ecoregions (n = 42):

- Aceros narcondami
- Acrocephalus familiaris
- Acrocephalus rehsei
- Acrocephalus rodericanus
- Acrocephalus sechellensis
- Acrocephalus vaughani
- Alauda razae
- Apalis fuscigularis
- Atlantisia rogersi
- Atlapetes pallidiceps
- Coccyzus ferrugineus
- Copsychus sechellarum
- Cyanoramphus cookie
- Ducula galeata
- Eudyptes robustus
- Foudia flavicans
- Foudia rubra
- Foudia sechellarum
- Fregata andrewsi
- Gallicolumba erythroptera
- Gallirallus sylvestris
- Haematopus chathamensis
- Leucopeza semperi
- Loxops caeruleirostris
- Mimus graysoni
- Mimus trifasciatus
- Morus capensis
- Nesospiza acunhae
- Nesospiza questi
- Nesospiza wilkinsi
- Nesotriccus ridgwayi
- Oceanodroma matsudairae
- Oceanodroma melania
- Pinaroloxias inornate
- Prosobonia cancellata
- Ramphocinclus brachyurus
- Sephanoides fernandensis
- Telespiza cantans
- Troglodytes tanneri
- Vini peruviana
- Zosterops griseovirescens
- Zosterops modestus

B) Species (n = 3) subsequently removed from the ecoregion species pools as they only exist in an ecoregion (Cocos Island) with fewer than nine species:

- Pinaroloxias inornata
- Nesotriccus ridgwayi
- Coccyzus ferrugineus"

C) Species that could not be manually assigned to either biomes or ecoregions (n = 29):

- Acrocephalus sorghophilus
- Calyptura cristata
- Campephilus principalis
- Carduelis hornemanni
- Catharacta lonnbergi
- Ceyx rufidorsa
- Chrysococcyx russatus
- Copsychus stricklandii
- Corvus levaillantii
- Cuculus optatus
- Eurochelidon sirintarae
- Falco pelegrinoides
- Gallirallus owstoni
- Himantopus leucocephalus
- Himantopus mexicanus
- Indicator conirostris
- Lanius marwitzi
- Larus thayeri
- Ortygospiza fuscocrissa
- Ortygospiza gabonensis
- Phalacrocorax carunculatus
- Ramphastos swainsonii
- Serpophaga munda
- Stachyris ambigua
- Sylvia althaea
- Sylvia minula
- Thraupis cyanoptera
- Trogon aurantiiventris
- Upucerthia jelskii

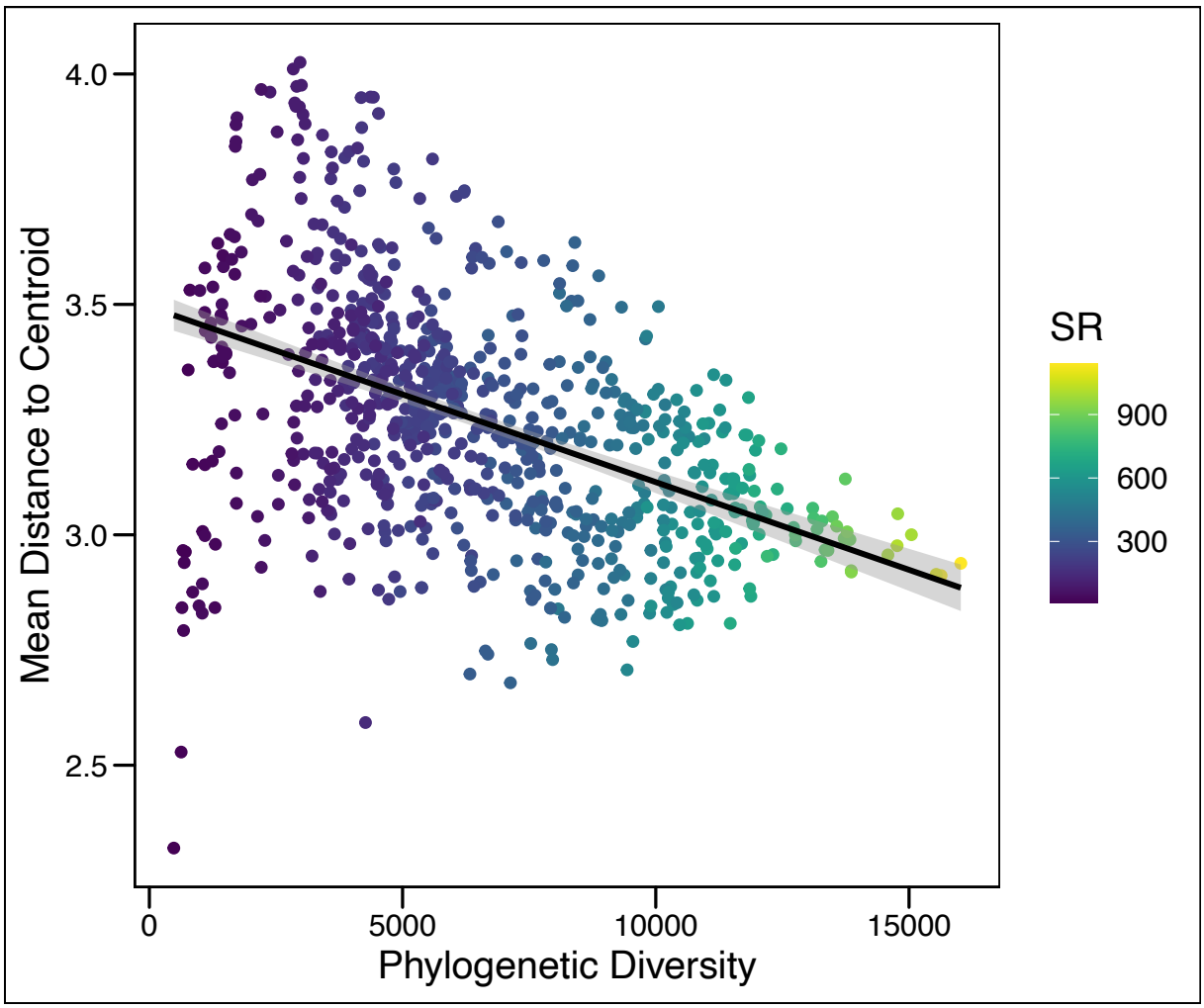

Figure S1: The phylogenetic diversity and mean distance to centroid value for each intact ecoregion community. Points are coloured by the number of species in each community, with yellow being the highest species richness (SR) and purple the lowest species richness.

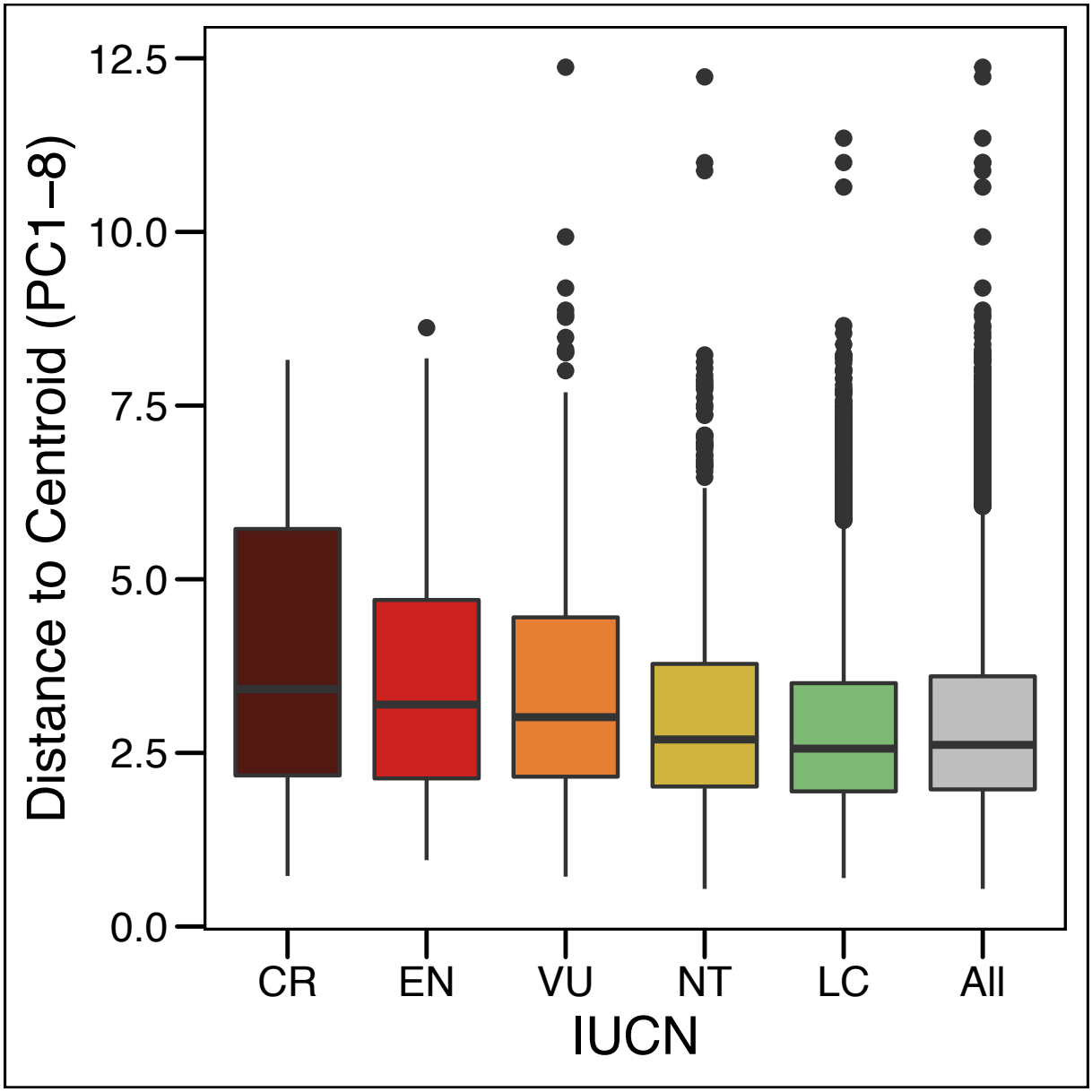

Figure S2: Distance to centroid scores for all global bird species (All) in each of the IUCN threat categories: critically endangered (CR), endangered (EN), vulnerable (VU), near threatened (NT) and least concern (LC). Box and whiskers show the median value, and interquartile range.

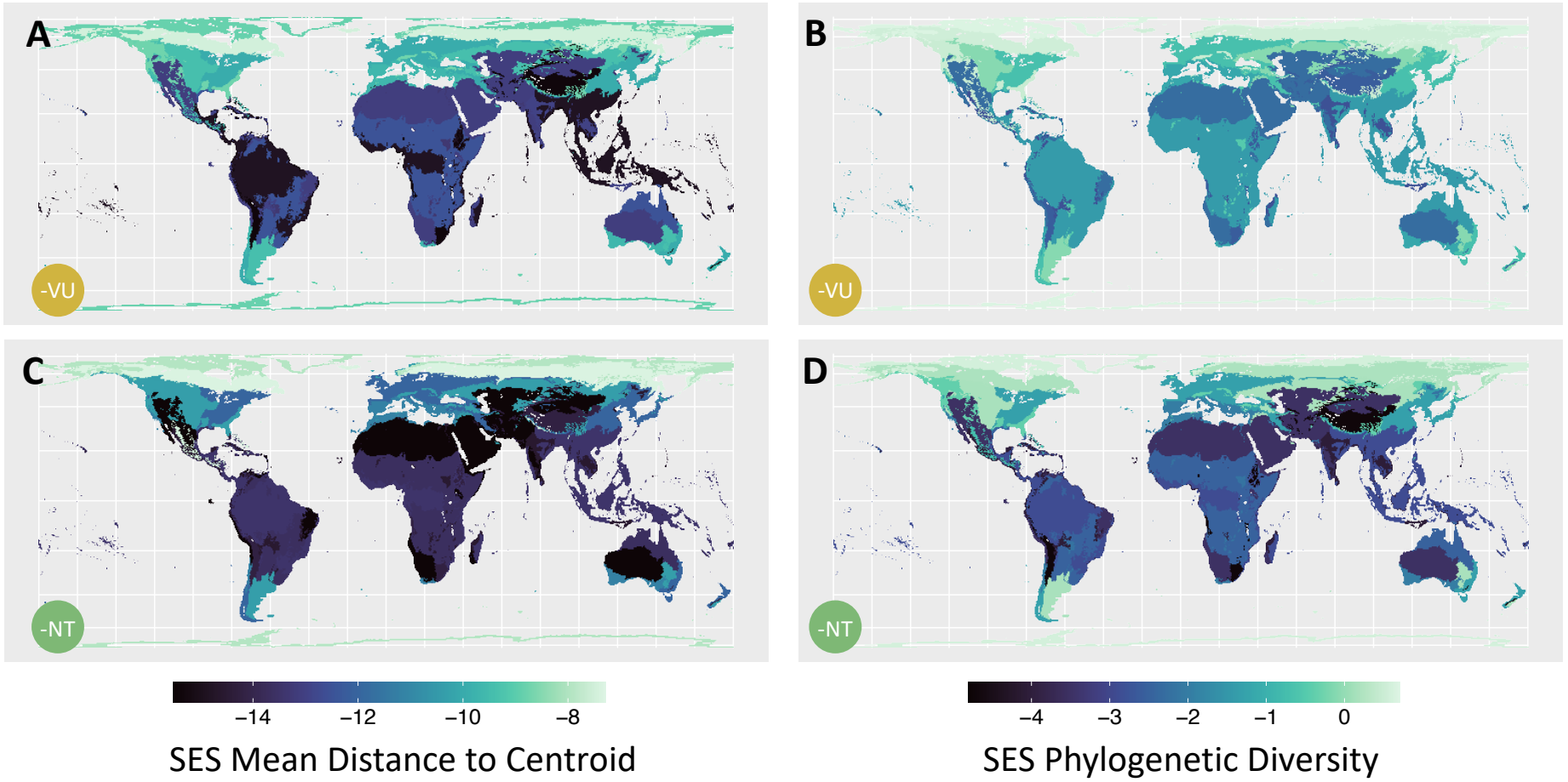

Figure S3: Standard effect sizes (SES) for A) morphological and B) phylogenetic diversity calculated after Critically Endangered, Endangered and Vulnerable (VU) species, and (C, D) additionally, when Near Threatened (NT) species are dropped from assemblages across 14 terrestrial biomes.

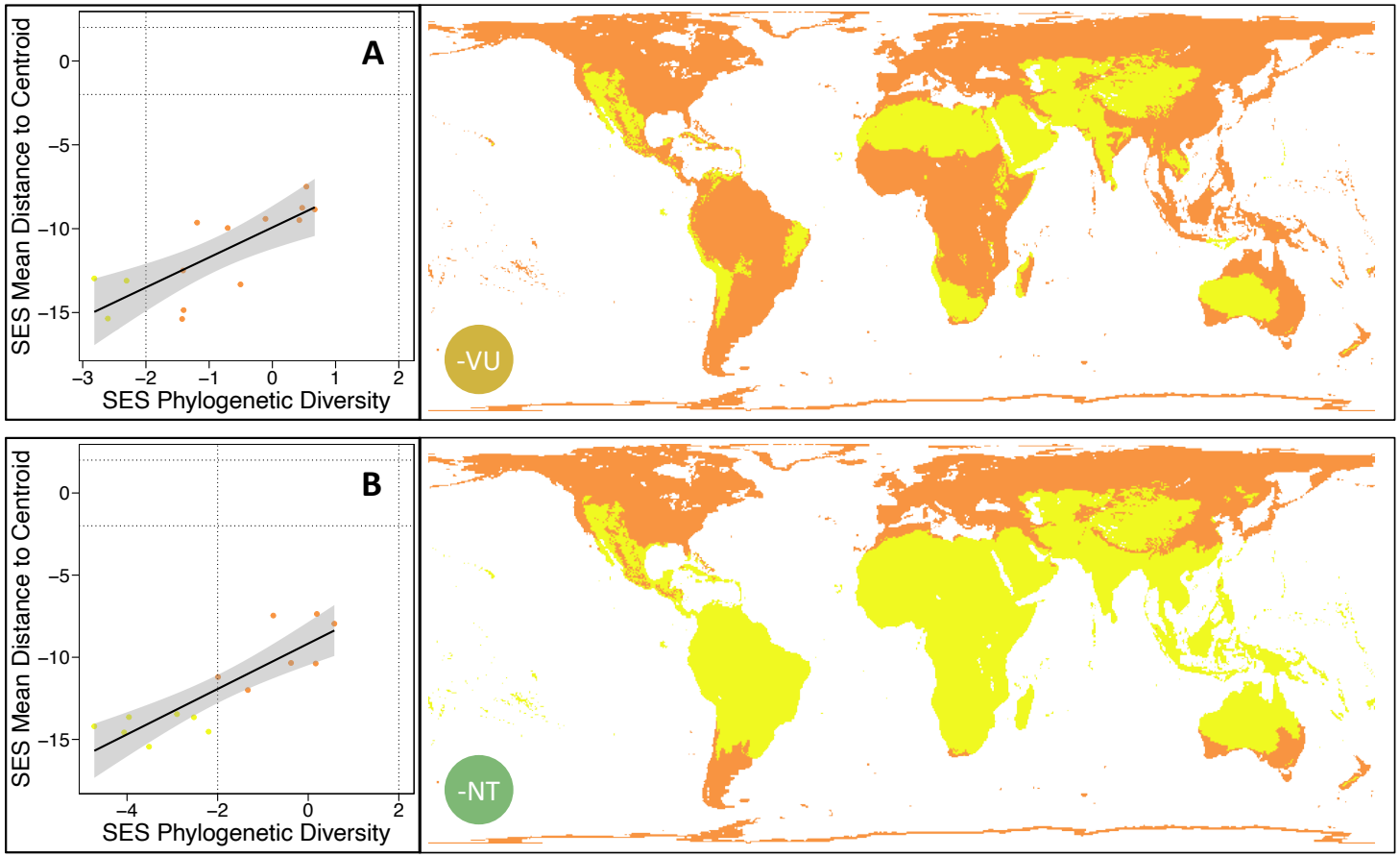

Figure S4: Standard effect sizes (SES) of morphological diversity (mean distance to centroid) and phylogenetic diversity calculated for species assemblages in each global terrestrial biome (n = 14) where significant deviation from expected (+/- 2) is present. Homogenisation is indicated where SES is more negative than -2. Panel A shows significant SES scores calculated where assemblages are missing Critically Endangered, Endangered and Vulnerable (VU) species, and panel B shows this were Near Threatened (NT) species are also missing. Dark grey indicates no significant deviation from expected.

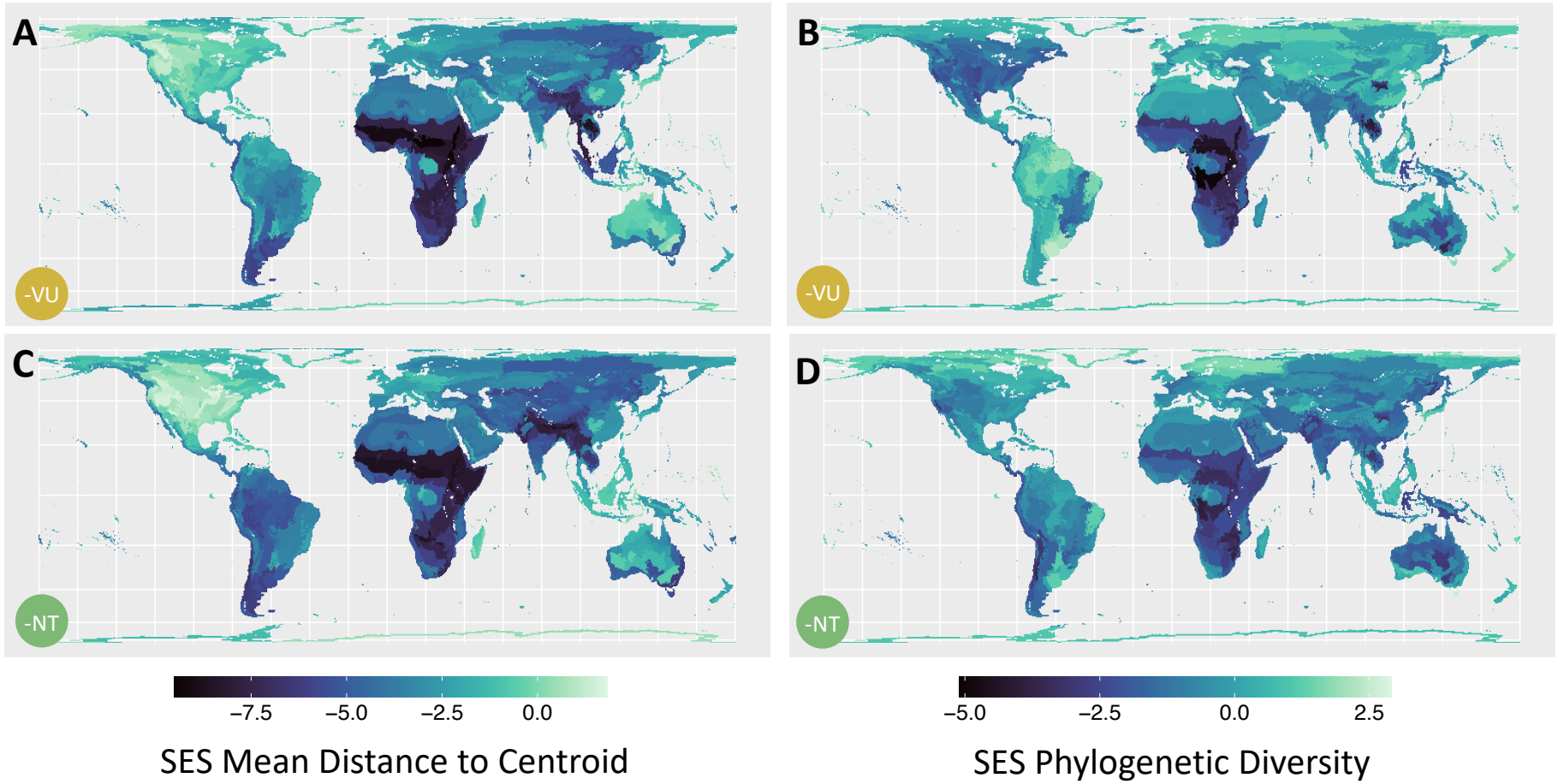

Figure S5: Standard effect sizes (SES) for A) morphological and B) phylogenetic diversity calculated after Critically Endangered, Endangered and Vulnerable (VU) species, and (C, D) additionally, when Near Threatened (NT) species are dropped from assemblages across 814 terrestrial ecoregions.

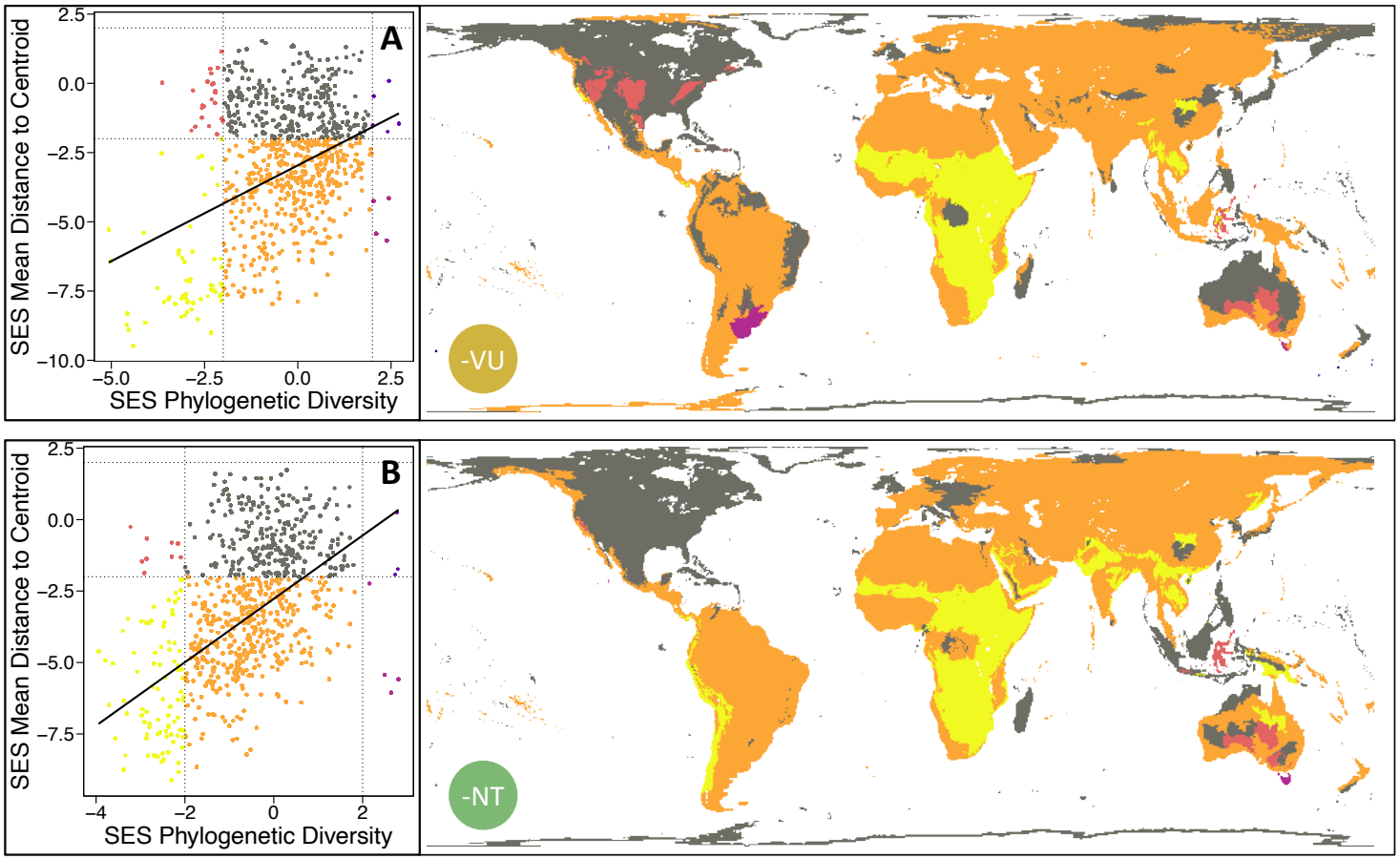

Figure S6: Standard effect sizes (SES) of morphological diversity (mean distance to centroid) and phylogenetic diversity calculated for species assemblages in each global terrestrial ecoregion (n = 814) where significant deviation from expected (+/- 2) is present. Homogenisation is indicated where SES is more negative than -2. Panel A shows significant SES scores calculated where assemblages are missing Critically Endangered, Endangered and Vulnerable (VU) species, and panel B shows this were Near Threatened (NT) species are also missing. Dark grey indicates no significant deviation from expected.

Table S1: a) SES morphological diversity (mean distance to centroid values) and b) SES phylogenetic diversity across different biomes where critically endangered (CR) and, additionally, endangered (EN) species are lost. SES values more negative than -2 indicate homogenisation.

a) Morphological Diversity (Mean Distance to Centroid)				
	CR Species Lost		**Plus EN Species Lost**	
Biome	**SES Score**	**Position**	**SES Score**	**Position**
Tropical dry forest	-8.800	1	-11.511	1
Tropical moist forest	-8.247	2	-10.725	3
Flooded grassland	-7.655	3	-10.046	6
Desert	-7.318	4	-10.139	5
Mangroves	-6.831	5	-10.661	4
Tropical coniferous forest	-6.663	6	-7.086	9
Temperate coniferous forest	-6.392	7	-8.369	7
Tropical grassland	-5.785	8	-8.295	8
Montane grassland	-5.558	9	-11.511	2
Boreal forest/taiga	-3.712	10	-5.646	13
Tundra	-3.223	11	-5.486	14
Temperate broadleaf forest	-3.056	12	-6.792	11
Mediterranean forest	-1.689	13	-6.310	12
Temperate grassland	-0.954	14	-6.859	10
b) Phylogenetic Diversity				
Mediterranean forest	-2.141	1	-1.158	3
Tropical dry forest	-1.549	2	-1.963	2
Temperate broadleaf forest	-1.083	3	-2.152	1
Temperate grassland	-0.992	4	0.397	10
Desert	-0.140	5	-0.009	8
Tropical moist forest	-0.137	6	-0.335	5
Tropical coniferous forest	0.143	7	0.674	12
Boreal forest/taiga	0.159	8	1.414	14
Temperate coniferous forest	0.171	9	0.477	11
Tundra	0.199	10	1.255	13
Tropical grassland	0.329	11	0.328	9
Flooded grassland	0.502	12	-0.207	6
Montane grassland	0.618	13	-0.637	4
Mangroves	0.859	14	-0.192	7

Table S2: Top 20 ecoregions containing species assemblages most threatened by phylogenetic and morphological homogenisation when losing critically endangered (CR) and endangered (EN) species. The a) SES morphological diversity (mean distance to centroid values) and b) SES phylogenetic diversity values are given.

a) Mean Distance to Centroid					
		CR Species Lost		**Plus EN Species Lost**	
Ecoregion	**Biome**	**SES Score**	**Position**	**SES Score**	**Position**
Himalayan subtropical broadleaf forests	Tropical moist forest	-6.917	1	-6.866	11
Eastern Himalayan alpine shrub and meadows	Montane grassland	-6.565	2	-8.239	2
Northern Triangle subtropical forests	Tropical moist forest	-6.477	3	-7.466	4
Eastern Himalayan subalpine conifer forests	Temperate coniferous forest	-6.367	4	-8.528	1
Terai-Duar savanna and grasslands	Tropical grassland	-6.269	5	-7.212	8
Northern Indochina subtropical forests	Tropical moist forest	-6.255	6	-6.180	17
Western Himalayan subalpine conifer forests	Temperate coniferous forest	-6.174	7	-7.381	5
Northeastern Himalayan subalpine conifer forests	Temperate coniferous forest	-6.089	8	-6.379	16
Central Indochina dry forests	Tropical dry forest	-6.016	9	-7.318	6
Eastern Himalayan broadleaf forests	Temperate broadleaf forest	-5.961	10	-7.911	3
Southeastern Indochina dry evergreen forests	Tropical dry forest	-5.833	11	-7.238	7
Brahmaputra Valley semi-evergreen forests	Tropical moist forest	-5.824	12	-6.957	10
Himalayan subtropical pine forests	Tropical coniferous forest	-5.806	13	-5.760	28
Northern Triangle temperate forests	Temperate broadleaf forest	-5.756	14	-6.152	18
Upper Gangetic Plains moist deciduous forests	Tropical moist forest	-5.736	15	-5.794	27
Nujiang Langcang Gorge alpine conifer and mixed forests	Temperate coniferous forest	-5.716	16	-6.759	12
Rwenzori-Virunga montane moorlands	Montane grassland	-5.607	17	-5.980	22
Lower Gangetic Plains moist deciduous forests	Tropical moist forest	-5.469	18	-6.691	13
Cameroonian Highlands forests	Tropical moist forest	-5.378	19	-4.509	87
Mizoram-Manipur-Kachin rain forests	Tropical moist forest	-5.368	20	-7.018	9
b) Phylogenetic Diversity					
Central Indochina dry forests	Tropical dry forest	-4.352	1	-3.854	1
Southeastern Indochina dry evergreen forests	Tropical dry forest	-4.005	2	-3.170	5
Tuamotu tropical moist forests	Tropical moist forest	-3.526	3	-2.453	19
Northwest Iberian montane forests	Mediterranean forest	-3.492	4	-2.926	10

Pyrenees conifer and mixed forests	Temperate broadleaf forest	-3.459	5	-2.873	11
Tonle Sap freshwater swamp forests	Tropical moist forest	-3.216	6	-1.801	43
Cardamom Mountains rain forests	Tropical moist forest	-3.124	7	-1.667	55
Tonle Sap-Mekong peat swamp forests	Tropical moist forest	-3.059	8	-1.657	56
Puerto Rican moist forests	Tropical moist forest	-2.711	9	-1.587	66
Meghalaya subtropical forests	Tropical moist forest	-2.56	10	-2.427	21
Marquesas tropical moist forests	Tropical moist forest	-2.515	11	-2.725	14
Murray-Darling woodlands and mallee	Mediterranean forest	-2.286	12	-3.534	2
Mitchell grass downs	Tropical grassland	-2.256	13	-3.125	6
Isthmian-Atlantic moist forests	Tropical moist forest	-2.251	14	-0.164	284
Isthmian-Pacific moist forests	Tropical moist forest	-2.231	15	-0.672	180
Sulawesi lowland rain forests	Tropical moist forest	-2.211	16	-1.364	90
Northwestern Hawaii scrub	Tropical grassland	-2.202	17	-0.209	23
Central American dry forests	Tropical dry forest	-2.139	18	-0.209	270
Talamancan montane forests	Tropical moist forest	-2.134	19	0.227	519
Costa Rican seasonal moist forests	Tropical moist forest	-2.112	20	-0.860	149

APPENDIX 3

Supplementary materials and methods for Chapter 4:

The effects of secondary forest regeneration on avian phylogenetic diversity.

Appendix S1: Justification for removal of studies from the original Sayer et al. (2017) meta-analysis dataset.

Care was taken to ensure that data from studies with large differences in sampling effort, unclear secondary forest ages or incomplete sampling of the avian community were re-extracted or excluded from our analyses.

Studies excluded:

- Hutto (1989): We were unable to confirm the secondary forest ages of 2 and 5 years. The secondary forest ages were taken from (Dunn and Romdal, 2005) who used the dataset. The age of secondary forest vegetation is not stated in (Hutto, 1989), but the height of the vegetation is given as 2 m and 5 m.
- Mallari et al. (2011): This study calculates density estimates for 18 key bird species in each habitat and therefore a comprehensive species list is not provided.
- Marsden et al. (2006): The data extracted is for 31 species that were recorded >50 times, and so the same species are observed in both primary and secondary forests, while a comprehensive species list is not provided.
- Terborgh and Weske (1969): Sampling effort is not quantifiable, but the description in text suggests that there are large differences in the sampling effort between primary and secondary forest sites, with primary forest sites sampled considerably more intensively. Primary forest sampling was conducted with higher net numbers, larger areas sampled, and more visits made.

Part of study excluded:

- Blake and Loiselle (2001): We have removed the older secondary forest site present in this study as the sampling effort was considerably less than for the other forest types (14 samples over 3 years for old secondary and 25 samples over 10 years for young secondary and primary forest). Furthermore, only mist nets were used as a sampling technique in old secondary forest compared to mist nets and point counts in primary and young secondary forest.

Re-extracted data:

- Borges (2007): The primary forest sites split back to the original three sites to ensure each is compared to one secondary forest site.
- Maas et al. (2009): Ensured sampling effort was equal: ungrouped the 2001/2 and 2008 site data and removed species recorded outside the point count area (50 m).
- Reid et al. (2012): Bird species that were described as 'opportunist detections' were removed from our analyses. Only species recorded during point counts are included in our dataset to maintain equal sampling effort.
- Gilroy et al. (2014): Data re-extracted to ensure that paired sites had equal numbers of sampling points in both primary and secondary forest sites.

Table S1: Studies extracted from Sayer et al. (2017). The location of sites in either the New or Old World, country of origin, number and age of secondary forest sites, number of primary forest sites, and distances between primary and secondary forest sites are given.

Reference	Location of sites	Country	Number of secondary forest sites	Age of secondary forest site(s) (years)	Number of primary forest sites	Distance to primary forest sites (metres)
Andrade and Rubio-Torgler (1994)	New World	Colombia	2	3, 11.5	1	0 (Continuous)
Banks-Leite et al. (2012)	New World	Brazil	1	50	1	0 (Continuous)
Barlow et al. (2007)	New World	Brazil	1	16.5	1	1725 (650-2800)
Becker and Ágreda (2005)	New World	Ecuador	1	17.5	1	1000 (1000+)
Becker et al. (2008)	New World	Ecuador	3	17.5, 17.5, 40	1	NA (Continuous and discontinuous)
Blake and Loiselle (2001)	New World	Costa Rica	1	5	1	0 (Continuous)
Borges (2007)	New World	Brazil	3	4.5, 11, 27.5	3	60 (Continuous 20-100)
Dawson et al. (2011)	Old World	Papua New Guinea	1	20	1	0 (Continuous)
Gilroy et al. (2014)	New World	Colombia	5	3, 8, 12, 25, 30	3	300 (>=300)
Johns (1991)	New World	Brazil	1	1	1	500 (Continuous and discontinuous 0-1000)
Maas et al. (2009)	Old World	Indonesia	3	3.5, 4, 5.5	3	0 (Implied continuous)
Mulwa et al. (2012)	Old World	Kenya	1	50	1	0 (Continuous)
Naidoo (2004)	Old World	Uganda	1	13	1	5000 (< 5000)
O'Dea and Whittaker (2007)	New World	Ecuador	1	17.5	1	0 (Continuous)
Raman et al. (1998)	Old World	India	5	1, 5, 10, 25, 100	1	0 (Continuous)
Reid et al. (2012)	New World	Costa Rica	1	9	1	0 (Continuous)
Renner et al. (2006)	New World	Guatemala	1	4	1	0 (Continuous)
Sodhi et al. (2005)	Old World	Indonesia	1	40	1	NA
Tvardíková (2010)	Old World	Papua New Guinea	1	7	1	4000 (approx. 4000)
Wijesinghe and Brooke (2005)	Old World	Sri Lanka	1	5	1	2000 (<2000)

Table S2: Full description of phylogenetic and beta diversity metrics used in this study.

Metric name	Abbreviation used in this study	Metric description	Equation	References
Phylogenetic diversity or Faith's phylogenetic diversity	PD	The sum of all branch lengths connecting species in a community or site. PD is measured in millions of years and is the total amount of evolutionary history represented by that community. The phylogeny used only contains species that are present in that particular assemblage. Therefore, adding species to a community will at the very least add a terminal branch to the phylogeny, and thus, PD and SR are expected to correlate.	$pd = \sum_{i}^{n} l_i$ Where l_i is the branch length of species i, and there are n species present in the community.	Faith (1992)
Standard effect size of PD	ses.PD	The observed PD of communities compared with the PD of null communities of equal SR, with species being randomly drawn from a regional species pool. In the present study, we compare against 999 null communities for all 500 phylogenetic trees. A positive ses.PD value indicates an observed community with higher than expected PD given SR, and a negative value lower than expected PD given SR.	$S.E.S = \frac{observed - \overline{null}}{sd\ (null)}$ The PD of our observed community minus the mean PD of the 999 null communities. This is then divided by the PD standard deviation of the null communities.	Swenson (2014)
Mean pairwise distance	MPD	The average phylogenetic distance between every combination of paired individuals in a community.	$mpd = \frac{\Sigma_i^n \Sigma_j^n \delta_{i,j}}{n}, where\ i\ \neq j$	Webb et al. (2002)

		High values of MPD indicate that the community is composed of species that diverged from each other a long time ago and so are more widely distributed across clades. In contrast, low values of MPD indicate that species in the community are phylogenetically clustered and distributed within clades having diverged from their common ancestors more recently.	Where there are n species in the community, and $\delta_{i,j}$ is the phylogenetic distance between species i and j.	
Standard effect size of MPD or NRI	ses.MPD	The observed MPD of communities compared with the MPD of null communities of equal SR, with species being randomly drawn from a regional species pool. In the present study, we compare against 999 null communities for all 500 phylogenetic trees. Positive values of ses.MPD suggests that MPD is higher than expected given SR, and negative values suggest that MPD is lower than expected given SR.	$S.E.S = \frac{observed - \overline{null}}{sd\ (null)}$ The MPD of our observed community minus the mean MPD of the 999 null communities. This is then divided by the MPD standard deviation of the null communities.	Webb et al. (2002)
Mean nearest taxon distance	MNTD	The average phylogenetic distance between an individual and its closest relative in the community. High values of MNTD indicate that the community does not contain species which are closely related to each other, whereas low MNTD values suggests that closely related species do reside in that community.	$mntd\ = \frac{\sum_i^n min\delta_{i,j}}{n}, where\ i \neq\ j$ Where there are n species in the community, and $min\delta_{i,j}$ is the minimum phylogenetic distance between species i and its most close relative j in the community.	Webb et al. (2002)
Standard effect size of MNTD or NTI	ses.MNTD	The observed MNTD of communities compared with the MNTD of null communities of equal SR, with species being randomly drawn from a regional species pool. In the present study, we compare against 999 null communities for all 500 phylogenetic trees.	$S.E.S = \frac{observed - \overline{null}}{sd\ (null)}$	Webb et al. (2002)

		Positive values suggest that MNTD is higher than expected given SR, and negative values suggest that MNTD is lower than expected given SR.	The MNTD of our observed community minus the mean MNTD of the 999 null communities. This is then divided by the MNTD standard deviation of the null communities.	
Phylogenetic beta diversity or Phylogenetic Sørenson's index	ßPD	Measures how similar two communities are in terms of their evolutionary history. In this instance, we measure phylogenetic similarity as a fraction of the phylogenetic branch-lengths present in secondary forest communities that were also present in paired primary forest communities using the phylogenetic Sørenson's index.	$PhyloSor = 2 \times \frac{BL_{ij}}{BL_i + BL_j}$ Where BL_{ij} are the branch lengths that are common to communities i and j. BL_i and BL_j are the total branch lengths (Faith's PD) present in communities i and j respectively.	Bryant et al. (2008; Graham and Fine (2008)
Beta diversity or Sørenson's index	ßTD	Measures how similar two communities are in terms of their species composition. We use the Sørenson's index to measure compositional intactness, that is, the fraction of taxa present in secondary forest communities that were also found in the paired primary forest communities.	$Sor = 2 \times \frac{S_{ij}}{S_i + S_j}$ Where S_{ij} is the number of taxa present in both communities i and j. S_i and S_j are the total number of species in communities i and j respectively.	Whittaker (1972, 1960)

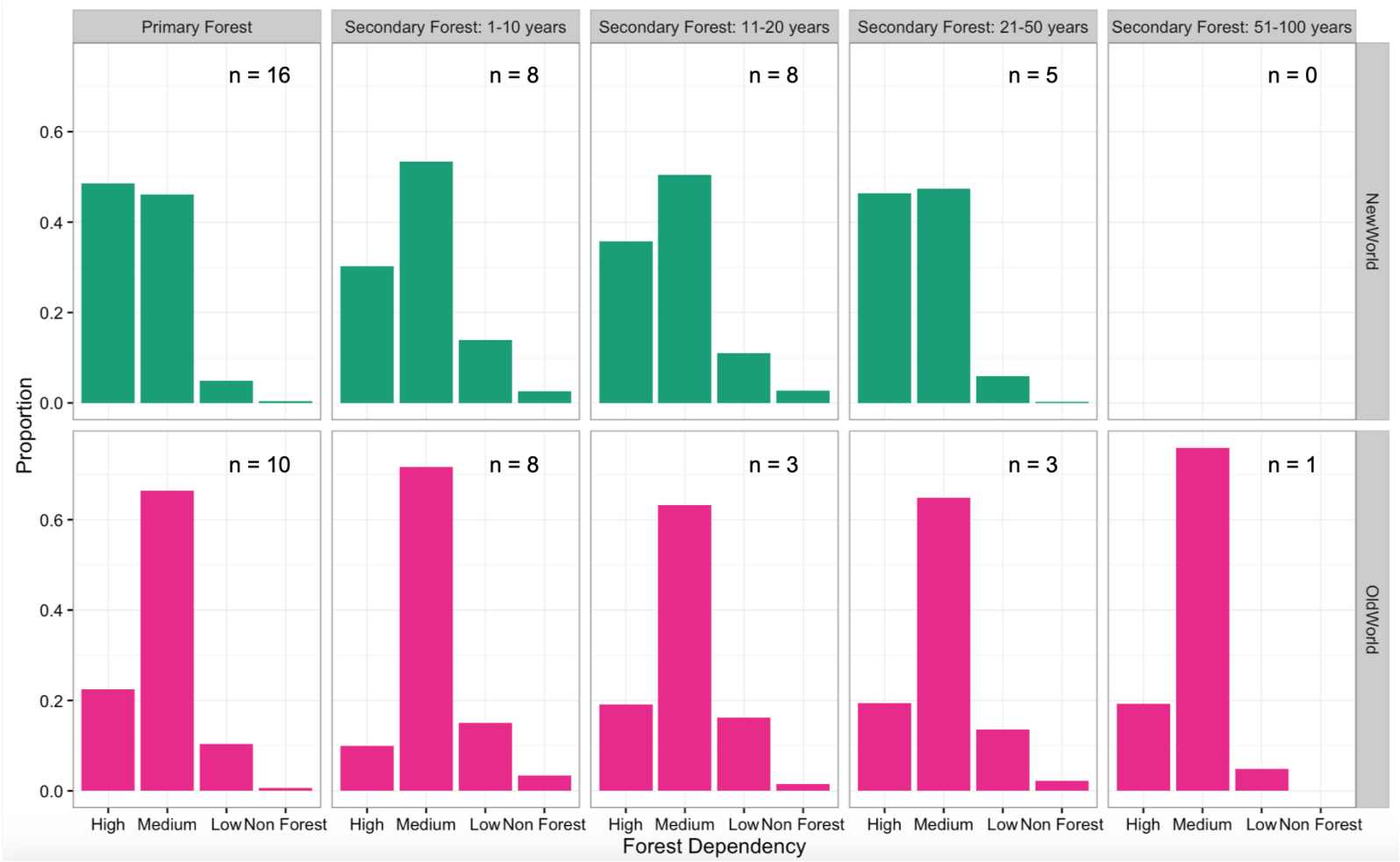

Figure S1: The proportion of species across all studies categorised by Birdlife International as having “High”, “Medium”, “Low” or “Non” forest dependency, that were observed in secondary forest of various ages (1-10 years, 11-20 years and 51-100 years) and primary forests, in the New (green) and Old World (pink).

Table S3: Models for sites in the Old World, New World and across all sites, constructed for testing the effects of primary versus secondary forests on the response variables listed. All species included in analysis.

Response	World Location	Model	Primary Forest Mean (± SE)	Secondary Forest Mean	LRT Statistic (χ^2)	p-value
SR	Old World	Habitat	64.82 ± 9.96	58.66	1.43	0.232
	New World	Habitat	97.63 ± 13.17	94.58	0.26	0.609
	All Sites	Habitat	84.52 ± 9.62	80.31	1.01	0.315
PD	Old World	Habitat	2156.50 ± 238.30	1927.40	2.63	0.105
	New World	Habitat	2488.41 ± 302.94	2406.39	0.52	0.469
	All Sites	Habitat	2355.60 ± 209.37	2216.54	2.45	0.118
ses.PD	Old World	Habitat	-3.59 ± 0.29	-3.82	0.52	0.469
	New World	Habitat	-4.89 ± 0.37	-4.90	<0.01	0.988
	All Sites	Habitat	-4.36 ± 0.28	-4.44	0.15	0.701
MPD	Old World	Habitat	135.61 ± 4.26	131.84	1.59	0.208
	New World	Habitat	129.32 ± 2.84	129.72	0.05	0.822
	All Sites	Habitat	131.79 ± 2.45	130.61	0.54	0.464
ses.MPD	Old World	Habitat	-3.11 ± 0.78	-3.52	1.49	0.222
	New World	Habitat	-4.37 ± 0.68	-4.16	0.25	0.617
	All Sites	Habitat	-3.88 ± 0.52	-3.90	0.01	0.933

MNTD	Old World	Habitat	49.44 ± 2.94	50.57	0.29	0.589
	New World	Habitat	34.03 ± 1.03	34.54	0.25	0.617
	All Sites	Habitat	40.16 ± 2.18	41.03	0.72	0.396
ses.MNTD	Old World	Habitat	-2.44 ± 0.23	48.03	0.12	0.727
	New World	Habitat	-3.74 ± 0.22	-3.71	0.02	0.890
	All Sites	Habitat	-3.20 ± 0.21	-3.23	0.04	0.846

a Model built containing observations from all study sites (i.e. includes those sites without data on distance to primary forest).

Table S4: Models for sites in the Old World, New World and across all sites, constructed for testing the effects of secondary forest age, and distance between paired secondary and primary forest sites, on species and phylogenetic community intactness.

Response	World Location	Observations (Group Size)	Model	Slope Estimate (± SE)	Term Dropped in LRT	LRT Statistic (χ^2)	p-value
ßTD	Old World	13 (7)	Age * Distance	Age:Distance: 0.15 ± 0.06	Interaction	4.36	0.037*
				Age: 0.24 ± 0.04			
				Distance: -0.11 ± 0.06			
		13 (7)	Age + Distance	Age: 0.25 ± 0.04	Age	16.68	<0.001***
				Distance: 0.02 ± 0.01	Distance	1.63	0.202
		13 (7)	Age	0.25 ± 0.05	Age	15.24	<0.001***
		13 (7)	Distance	0.01 ± 0.03	Distance	0.19	0.665
		14 (8)[a]	Age	0.25 ± 0.04	Age	17.71	<0.001***
	New World	18 (11)	Age * Distance	Age:Distance: 0.05 ± 0.04	Interaction	1.16	0.281
				Age: -0.07 ± 0.09			
				Distance: -0.10 ± 0.05			
		18 (11)	Age + Distance	Age: 0.01 ± 0.06	Age	0.05	0.824
				Distance: -0.05 ± 0.02	Distance	4.64	0.031*
		18 (11)	Age	0.17 ± 0.05	Age	0.85	0.357
		18 (11)	Distance	-0.05 ± 0.02	Distance	5.43	0.020*
		21 (12)[a]	Age	-0.01 ± 0.07	Age	0.01	0.923

	All Sites	31 (18)	Age * Distance	Age:Distance: -0.02 ± 0.03 Age: 0.20 ± 0.04 Distance: <0.01 ± 0.04	Interaction	0.22	0.639
		31 (18)	Age + Distance	Age: 0.19 ± 0.04 Distance: -0.01 ± 0.02	Age Distance	8.60 0.37	0.003** 0.542
		31 (18)	Age	0.20 ± 0.04	Age	9.22	0.002**
		31 (18)	Distance	-0.02 ± 0.02		0.99	0.320
		35 (20)[a]	Age	0.19 ± 0.04	Age	8.16	0.004**
ßPD	Old World	13 (7)	Age * Distance	Age:Distance: 0.13 ± 0.05 Age: 0.21 ± 0.03 Distance: -0.10 ± 0.05	Interaction	5.02	0.025*
		13 (7)	Age + Distance	Age: 0.22 ± 0.03 Distance: 0.02 ± 0.01	Age Distance	18.33 1.72	<0.001*** 0.189
		13 (7)	Age	0.22 ± 0.04	Age	16.77	<0.001***
		13 (7)	Distance	0.01 ± 0.02	Distance	0.16	0.685
		14 (8)[a]	Age	0.23 ± 0.03	Age	19.51	<0.001***
	New World	18 (11)	Age * Distance	Age:Distance: 0.04 ± 0.04 Age: -0.07 ± 0.07 Distance: -0.07 ± 0.04	Interaction	1.44	0.230

	18 (11)	Age + Distance	Age: 0.01 ± 0.05	Age	0.02	0.901
			Distance: -0.03 ± 0.02	Distance	3.31	0.069
	18 (11)	Age	0.00 ± 0.05	Age	<0.01	0.954
	18 (11)	Distance	-0.03 ± 0.02	Distance	3.30	0.069
	21 (12)[a]	Age	-0.01 ± 0.06	Age	0.05	0.827
All Sites	31 (18)	Age * Distance	Age:Distance: -0.02 ± 0.03	Interaction	0.53	0.466
			Age: 0.13 ± 0.05			
			Distance: 0.02 ± 0.03			
	31 (18)	Age + Distance	Age: 0.15 ± 0.03	Age	8.15	0.004**
			Distance: -0.01 ± 0.02	Distance	0.18	0.671
	31 (18)	Age	0.15 ± 0.03	Age	8.23	0.004**
	31 (18)	Distance	-0.01 ± 0.01	Distance	0.26	0.611
	35 (20)[a]	Age	0.15 ± 0.04	Age	7.85	0.005**

a Model built containing observations from all study sites (i.e. includes those sites without data on distance to primary forest).

Table S5: Models for sites in the Old World, New World and across all sites, constructed for testing the effects of secondary forest age, and distance between paired secondary and primary forest sites, on the response variables listed. Species that do not normally occur in forest were excluded from analysis.

Response	**World Location**	**Observations (Group Size)**	**Model**	**Slope Estimate (± SE)**	**Term dropped in LRT**	**LRT Statistic (χ^2)**	**p-value**
Relative SR	Old World	13 (7)	Age * Distance	Age:Distance: 0.17 ± 0.07 Age: 0.12 ± 0.04 Distance: -0.14 ± 0.07	Interaction	4.76	0.029*
		13 (7)	Age + Distance	Age: 0.13 ± 0.05 Distance: 0.01 ± 0.02	Age Distance	5.75 0.58	0.017* 0.446
		13 (7)	Age	0.13 ± 0.05	Age	5.35	0.021*
		13 (7)	Distance	0.01 ± 0.02	Distance	0.19	0.663
		14 (8)[a]	Age	0.13 ± 0.05	Age	6.39	0.011*
	New World	18 (11)	Age * Distance	Age:Distance: 0.05 ± 0.04 Age: -0.10 ± 0.08	Interaction	1.83	0.177

				Distance: -0.08 ± 0.04			
		18 (11)	Age + Distance	Age: -0.01 ± 0.05	Age	0.06	0.801
				Distance: -0.03 ± 0.02	Distance	1.81	0.178
		18 (11)	Age	0.03 ± 0.05	Age	0.18	0.675
		18 (11)	Distance	-0.03 ± 0.02	Distance	1.92	0.166
		21 (12)[a]	Age	0.01 ± 0.07	Age	0.01	0.928
	All Sites	31 (18)	Age * Distance	Age:Distance: 0.01 ± 0.03	Interaction	0.12	0.732
				Age: 0.07 ± 0.05			
				Distance: -0.01 ± 0.03			
		31 (18)	Age + Distance	Age: 0.08 ± 0.04	Age	2.95	0.086
				Distance: -0.00 ± 0.02	Distance	0.06	0.800
		31 (18)	Age	0.08 ± 0.04	Age	2.97	0.085
		31 (18)	Distance	-0.00 ± 0.01	Distance	0.09	0.768
		35 (20)[a]	Age	0.08 ± 0.04	Age	2.22	0.137
Relative PD	Old World	13 (7)	Age * Distance	Age:Distance: 0.12 ± 0.07	Interaction	2.50	0.114

			Age: 0.07 ± 0.04 Distance: -0.10 ± 0.07			
	13 (7)	Age + Distance	Age: 0.08 ± 0.04	Age	3.19	0.074
			Distance: 0.01 ± 0.02	Distance	0.17	0.678
	13 (7)	Age	0.08 ± 0.04	Age	3.07	0.080
	13 (7)	Distance	0.00 ± 0.02	Distance	0.05	0.821
	14 (8)[a]	Age	0.09 ± 0.04	Age	4.01	0.045*
New World	18 (11)	Age * Distance	Age:Distance: 0.04 ± 0.03	Interaction	1.54	0.214
			Age: -0.07 ± 0.06 Distance: -0.06 ± 0.03			
	18 (11)	Age + Distance	Age: -0.01 ± 0.04	Age	0.04	0.848
			Distance: -0.02 ± 0.01	Distance	1.70	0.193
	18 (11)	Age	0.02 ± 0.04	Age	0.13	0.722
	18 (11)	Distance	-0.02 ± 0.01	Distance	1.79	0.181
	21 (12)[a]	Age	0.02 ± 0.05	Age	0.08	0.782

	All Sites	31 (18)	Age * Distance	Age:Distance: 0.01 ± 0.03 Age: 0.03 ± 0.04 Distance: -0.01 ± 0.03	Interaction	0.19	0.663
		31 (18)	Age + Distance	Age: 0.04 ± 0.03 Distance: -0.00 ± 0.01	Age Distance	1.55 0.08	0.213 0.778
		31 (18)	Age	0.04 ± 0.03	Age	1.55	0.213
		31 (18)	Distance	-0.00 ± 0.01	Distance	0.08	0.783
		35 (20)[a]	Age	0.04 ± 0.04	Age	1.24	0.266
Relative ses.PD	Old World	13 (7)	Age * Distance	Age:Distance: -0.79 ± 0.94 Age: -1.04 ± 0.54 Distance: 0.51 ± 0.87	Interaction	0.69	0.405
		13 (7)	Age + Distance	Age: -1.12 ± 0.54 Distance: -0.21 ± 0.19	Age Distance	3.67 1.17	0.056 0.280
		13 (7)	Age	-1.07 ± 0.57	Age	3.14	0.076
		13 (7)	Distance	-0.17 ± 0.21	Distance	0.642	0.423

	14 (8)[a]	Age	-0.89 ± 0.54	Age	2.52	0.112
New World	18 (11)	Age * Distance	Age:Distance: -0.27 ± 0.37	Interaction	0.45	0.504
			Age: 0.24 ± 0.77			
			Distance: 0.36 ± 0.43			
	18 (11)	Age + Distance	Age: -0.28 ± 0.38	Age	0.46	0.498
			Distance: 0.09 ± 0.23	Distance	0.15	0.697
	18 (11)	Age	-0.29 ± 0.38	Age	0.50	0.480
	18 (11)	Distance	0.10 ± 0.23	Distance	0.19	0.663
	21 (12)[a]	Age	-0.28 ± 0.39	Age	0.41	0.524
All Sites	31 (18)	Age * Distance	Age:Distance: 0.12 ± 0.30	Interaction	0.17	0.680
			Age: -0.79 ± 0.42			
			Distance: -0.17 ± 0.33			
	31 (18)	Age + Distance	Age: -0.69 ± 0.35	Age	3.14	0.076
			Distance: -0.05 ± 0.17	Distance	0.08	0.780
	31 (18)	Age	-0.68 ± 0.35	Age	3.07	0.080

		31 (18)	Distance	-0.01 ± 0.16	Distance	0.00	0.945
		35 (20)[a]	Age	0.04 ± 0.04	Age	2.59	0.107
Relative MPD	Old World	13 (7)	Age * Distance	Age:Distance: -0.01 ± 0.02 Age: 0.01 ± 0.01 Distance: 0.02 ± 0.02	Interaction	0.52	0.470
		13 (7)	Age + Distance	Age: 0.01 ± 0.01 Distance: 0.00 ± 0.00	Age Distance	0.67 1.10	0.412 0.293
		13 (7)	Age	0.01 ± 0.01	Age	0.50	0.480
		13 (7)	Distance	0.00 ± 0.00	Distance	0.93	0.335
		14 (8)[a]	Age	0.01 ± 0.01	Age	0.89	0.346
	New World	18 (11)	Age * Distance	Age:Distance: 0.00 ± 0.01 Age: -0.02 ± 0.02 Distance: -0.00 ± 0.01	Interaction	0.05	0.828
		18 (11)	Age + Distance	Age: -0.01 ± 0.01 Distance: -0.00 ± 0.00	Age Distance	2.89 0.09	0.089 0.771

		18 (11)	Age	-0.01 ± 0.01	Age	2.85	0.091
		18 (11)	Distance	-0.00 ± 0.01	Distance	0.05	0.826
		21 (12)[a]	Age	-0.01 ± 0.01	Age	1.36	0.244
	All Sites	31 (18)	Age * Distance	Age:Distance: -0.01 ± 0.01	Interaction	0.62	0.430
				Age: -0.00 ± 0.01			
				Distance: 0.01 ± 0.01			
		31 (18)	Age + Distance	Age: -0.01 ± 0.01	Age	0.43	0.511
				Distance: 0.00 ± 0.00	Distance	0.03	0.874
		31 (18)	Age	-0.01 ± 0.01	Age	0.45	0.503
		31 (18)	Distance	0.00 ± 0.00	Distance	0.04	0.838
		35 (20)[a]	Age	-0.005 ± 0.01	Age	0.38	0.536
Relative ses.MPD	Old World	13 (7)	Age * Distance	Age:Distance: -1.27 ± 1.13	Interaction	1.20	0.273
				Age: -0.17 ± 0.65			
				Distance: 1.23 ± 1.04			
		13 (7)	Age + Distance	Age: -0.29 ± 0.67	Age	0.18	0.668

			Distance: 0.09 ± 0.23	Distance	0.14	0.705
	13 (7)	Age	-0.31 ± 0.67	Age	0.21	0.645
	13 (7)	Distance	0.10 ± 0.23	Distance	0.17	0.679
	14 (8)[a]	Age	-0.15 ± 0.63	Age	0.06	0.805
New World	18 (11)	Age * Distance	Age:Distance: -0.39 ± 0.55	Interaction	0.48	0.487
			Age: -0.53 ± 1.15			
			Distance: 0.47 ± 0.63			
	18 (11)	Age + Distance	Age: -1.23 ± 0.58	Age	3.92	0.048*
			Distance: 0.09 ± 0.33	Distance	0.07	0.798
	18 (11)	Age	-1.24 ± 0.58	Age	3.95	0.047*
	18 (11)	Distance	0.11 ± 0.36	Distance	0.09	0.762
	21 (12)[a]	Age	-1.20 ± 0.54	Age	4.40	0.040*
All Sites	31 (18)	Age * Distance	Age:Distance: -0.54 ± 0.41	Interaction	1.65	0.199
			Age: -0.33 ± 0.59			
			Distance: 0.59 ± 0.45			

		31 (18)	Age + Distance	Age: -0.76 ± 0.50	Age	2.21	0.137
				Distance: 0.07 ± 0.22	Distance	0.11	0.741
		31 (18)	Age	-0.77 ± 0.50	Age	2.28	0.131
		31 (18)	Distance	0.10 ± 0.23	Distance	0.18	0.667
		35 (20)[a]	Age	-0.76 ± 0.46	Age	2.58	0.108
Relative MNTD	Old World	13 (7)	Age * Distance	Age:Distance: -0.09 ± 0.04	Interaction	3.84	0.050
				Age: -0.06 ± 0.02			
				Distance: 0.07 ± 0.04			
		13 (7)	Age + Distance	Age: -0.07 ± 0.03	Age	5.01	0.025*
				Distance: -0.02 ± 0.01	Distance	1.84	0.175
		13 (7)	Age	-0.07 ± 0.03	Age	4.53	0.033*
		13 (7)	Distance	-0.01 ± 0.01	Distance	1.36	0.244
		14 (8)[a]	Age	-0.06 ± 0.03	Age	4.31	0.038*
	New World	18 (11)	Age * Distance	Age:Distance: -0.01 ± 0.02	Interaction	0.17	0.683
				Age: 0.02 ± 0.04			

				Distance: 0.01 ± 0.02			
		18 (11)	Age + Distance	Age: 0.01 ± 0.02	Age	0.03	0.853
				Distance: 0.00 ± 0.01	Distance	0.03	0.852
		18 (11)	Age	0.00 ± 0.02	Age	0.02	0.892
		18 (11)	Distance	0.00 ± 0.01	Distance	0.02	0.890
		21 (12)[a]	Age	0.01 ± 0.02	Age	0.14	0.704
	All Sites	31 (18)	Age * Distance	Age:Distance: 0.01 ± 00.01	Interaction	0.79	0.374
				Age: -0.05 ± 00.02			
				Distance: -0.02 ± 00.02			
		31 (18)	Age + Distance	Age: -0.04 ± 00.02	Age	3.27	0.071
				Distance: -0.01 ± 00.01	Distance	0.646	0.422
		31 (18)	Age	-0.04 ± 00.02	Age	3.01	0.083
		31 (18)	Distance	-0.00 ± 00.01	Distance	0.38	0.535
		35 (20)[a]	Age	-0.03 ± 0.02	Age	0.15	0.148
Relative ses.MNTD	Old World	13 (7)	Age * Distance	Age:Distance: -0.96 ± 0.82	Interaction	1.29	0.256

			Age: -0.93 ± 0.47			
			Distance: 0.53 ± 0.76			
	13 (7)	Age + Distance	Age: -1.02 ± 0.49	Age	3.78	0.052
			Distance: -0.34 ± 0.17	Distance	2.74	0.098
	13 (7)	Age	-0.85 ± 0.46	Age	2.94	0.087
	13 (7)	Distance	-0.31 ± 0.19	Distance	1.90	0.169
	14 (8)[a]	Age	-0.75 ± 0.45	Age	2.45	0.118
New World	18 (11)	Age * Distance	Age:Distance: 0.12 ± 0.32	Interaction	0.12	0.729
			Age: 0.03 ± 0.66			
			Distance: -0.16 ± 0.36			
	18 (11)	Age + Distance	Age: 0.26 ± 0.36	Age	0.39	0.532
			Distance: -0.04 ± 0.17	Distance	0.06	0.802
	18 (11)	Age	0.27 ± 0.36	Age	0.42	0.518
	18 (11)	Distance	-0.05 ± 0.18	Distance	0.09	0.764
	21 (12)[a]	Age	0.32 ± 0.36	Age	0.66	0.418

All Sites	31 (18)	Age * Distance	Age:Distance: 0.34 ± 0.25	Interaction	1.88	0.171
			Age: -0.68 ± 0.34			
			Distance: -0.50 ± 0.28			
	31 (18)	Age + Distance	Age: -0.42 ± 0.29	Age	1.73	0.188
			Distance: -0.17 ± 0.15	Distance	1.31	0.253
	31 (18)	Age	-0.40 ± 0.30	Age	1.52	0.218
	31 (18)	Distance	-0.15 ± 0.15	Distance	1.09	0.296
	35 (20)[a]	Age	-0.33 ± 0.29	Age	1.09	0.296

a Model built containing observations from all study sites (i.e. includes those sites without data on distance to primary forest).

Table S6: Models for sites in the Old World, New World and across all sites, constructed for testing the effects of secondary forest age, and distance between paired secondary and primary forest sites, on the response variables listed. All species included in analysis.

Response	World Location	Observations (Group Size)	Model	Slope Estimate (± SE)	Term dropped in LRT	LRT Statistic (χ^2)	p-value
Relative SR	Old World	13 (7)	Age * Distance	Age:Distance: 0.16 ± 0.08	Interaction	3.68	0.055
				Age: 0.11 ± 0.05			
				Distance: -0.14 ± 0.07			
		13 (7)	Age + Distance	Age: 0.12 ± 0.05	Age	4.61	0.032*
				Distance: 0.01 ± 0.02	Distance	0.51	0.473
		13 (7)	Age	0.12 ± 0.05	Age	4.29	0.038*
		13 (7)	Distance	0.01 ± 0.02	Distance	0.19	0.660
		14 (8)[a]	Age	0.12 ± 0.05	Age	5.09	0.024*
	New World	18 (11)	Age * Distance	Age:Distance: 0.05 ± 0.04	Interaction	1.94	0.164
				Age: -0.11 ± 0.08			
				Distance: -0.08 ± 0.04			
		18 (11)	Age + Distance	Age: -0.02 ± 0.05	Age	0.13	0.721
				Distance: -0.03 ± 0.02	Distance	1.59	0.208
		18 (11)	Age	0.03 ± 0.05	Age	0.18	0.671
		18 (11)	Distance	-0.03 ± 0.02	Distance	1.64	0.200
		21 (12)[a]	Age	0.00 ± 0.06	Age	<0.01	0.967

	All Sites	31 (18)	Age * Distance	Age:Distance: 0.01 ± 0.03 Age: 0.06 ± 0.05 Distance: -0.01 ± 0.03	Interaction	0.10	0.747
		31 (18)	Age + Distance	Age: 0.07 ± 0.04 Distance: -0.00 ± 0.02	Age Distance	2.19 0.05	0.139 0.815
		31 (18)	Age	0.07 ± 0.04	Age	2.19	0.139
		31 (18)	Distance	-0.00 ± 0.01	Distance	0.06	0.803
		35 (20)[a]	Age	0.07 ± 0.05	Age	1.68	0.195
Relative PD	Old World	13 (7)	Age * Distance	Age:Distance: 0.12 ± 0.07 Age: 0.07 ± 0.04 Distance: -0.10 ± 0.07	Interaction	2.44	0.118
		13 (7)	Age + Distance	Age: 0.08 ± 0.05 Distance: 0.01 ± 0.02	Age Distance	2.50 0.15	0.114 0.701
		13 (7)	Age	0.08 ± 0.05	Age	2.41	0.121
		13 (7)	Distance	0.00 ± 0.02	Distance	0.05	0.824
		14 (8)[a]	Age	0.08 ± 0.04	Age	3.11	0.078
	New World	18 (11)	Age * Distance	Age:Distance: 0.04 ± 0.03 Age: -0.07 ± 0.06 Distance: -0.06 ± 0.03	Interaction	1.67	0.197
		18 (11)	Age + Distance	Age: -0.01 ± 0.04	Age	0.09	0.762

				Distance: -0.02 ± 0.01	Distance	1.64	0.201
		18 (11)	Age	0.02 ± 0.04	Age	0.12	0.726
		18 (11)	Distance	-0.02 ± 0.01	Distance	1.67	0.197
		21 (12)[a]	Age	0.02 ± 0.05	Age	0.05	0.819
	All Sites	31 (18)	Age * Distance	Age:Distance: 0.01 ± 0.03	Interaction	0.18	0.671
				Age: 0.03 ± 0.04			
				Distance: -0.01 ± 0.03			
		31 (18)	Age + Distance	Age: 0.04 ± 0.03	Age	1.12	0.290
				Distance: -0.00 ± 0.01	Distance	0.08	0.784
		31 (18)	Age	0.04 ± 0.03	Age	1.10	0.294
		31 (18)	Distance	-0.00 ± 0.01	Distance	0.06	0.808
		35 (20)[a]	Age	0.04 ± 0.04	Age	0.89	0.345
Relative ses.PD	Old World	13 (7)	Age * Distance	Age:Distance: -0.47 ± 0.75	Interaction	0.39	0.535
				Age: -1.04 ± 0.43			
				Distance: 0.23 ± 0.69			
		13 (7)	Age + Distance	Age: -1.09 ± 0.43	Age	5.21	0.022*
				Distance: -0.20 ± 0.15	Distance	1.66	0.197
		13 (7)	Age	-1.04 ± 0.46	Age	4.36	0.037*
		13 (7)	Distance	-0.16 ± 0.18	Distance	0.82	0.366
		14 (8)[a]	Age	-0.90 ± 0.43	Age	3.75	0.053

	New World	18 (11)	Age * Distance	Age:Distance: -0.20 ± 0.39	Interaction	0.21	0.649
				Age: -0.08 ± 0.82			
				Distance: 0.27 ± 0.46			
		18 (11)	Age + Distance	Age: -0.49 ± 0.39	Age	1.04	0.308
				Distance: 0.07 ± 0.25	Distance	0.08	0.781
		18 (11)	Age	-0.50 ± 0.39	Age	1.10	0.295
		18 (11)	Distance	0.09 ± 0.24	Distance	0.14	0.711
		21 (12)[a]	Age	-0.45 ± 0.42	Age	0.72	0.395
	All Sites	31 (18)	Age * Distance	Age:Distance: 0.10 ± 0.26	Interaction	0.17	0.683
				Age: -0.82 ± 0.35			
				Distance: -0.17 ± 0.30			
		31 (18)	Age + Distance	Age: -0.74 ± 0.29	Age	4.62	0.032*
				Distance: -0.06 ± 0.17	Distance	0.15	0.701
		31 (18)	Age	-0.73 ± 0.29	Age	4.50	0.034*
		31 (18)	Distance	-0.03 ± 0.16	Distance	0.03	0.873
		35 (20)[a]	Age	-0.68 ± 0.29	Age	3.72	0.054
Relative MPD	Old World	13 (7)	Age * Distance	Age:Distance: -0.00 ± 0.02	Interaction	0.07	0.785
				Age: 0.01 ± 0.01			
				Distance: 0.01 ± 0.02			
		13 (7)	Age + Distance	Age: 0.01 ± 0.01	Age	0.44	0.505

			Distance: 0.00 ± 0.00	Distance	0.60	0.437
	13 (7)	Age	0.01 ± 0.01	Age	0.35	0.555
	13 (7)	Distance	0.00 ± 0.00	Distance	0.51	0.476
	14 (8)[a]	Age	0.01 ± 0.01	Age	0.68	0.410
New World	18 (11)	Age * Distance	Age:Distance: 0.00 ± 0.01	Interaction	0.05	0.826
			Age: -0.02 ± 0.02			
			Distance: -0.00 ± 0.01			
	18 (11)	Age + Distance	Age: -0.01 ± 0.01	Age	2.69	0.101
			Distance: -0.00 ± 0.01	Distance	0.08	0.771
	18 (11)	Age	-0.01 ± 0.01	Age	2.66	0.103
	18 (11)	Distance	-0.00 ± 0.01	Distance	0.05	0.826
	21 (12)[a]	Age	-0.01 ± 0.01	Age	1.27	0.259
All Sites	31 (18)	Age * Distance	Age:Distance: -0.01 ± 0.01	Interaction	0.58	0.447
			Age: -0.00 ± 0.01			
			Distance: 0.01 ± 0.01			
	31 (18)	Age + Distance	Age: -0.00 ± 0.01	Age	0.36	0.550
			Distance: 0.00 ± 0.00	Distance	<0.01	0.985
	31 (18)	Age	-0.00 ± 0.01	Age	0.36	0.548
	31 (18)	Distance	0.00 ± 0.00	Distance	<0.01	0.953
	35 (20)[a]	Age	-0.00 ± 0.01	Age	0.30	0.584

Relative ses.MPD	Old World	13 (7)	Age * Distance	Age:Distance: -0.80 ± 0.90	Interaction	0.77	0.380
				Age: -0.51 ± 0.51			
				Distance: 0.71 ± 0.83			
		13 (7)	Age + Distance	Age: -0.59 ± 0.52	Age	1.22	0.270
				Distance: -0.02 ± 0.18	Distance	0.01	0.930
		13 (7)	Age	-0.59 ± 0.52	Age	1.21	0.271
		13 (7)	Distance	0.00 ± 0.19	Distance	<0.01	0.994
		14 (8)[a]	Age	-0.45 ± 0.49	Age	0.80	0.370
	New World	18 (11)	Age * Distance	Age:Distance: 0.12 ± 0.63	Interaction	0.02	0.887
				Age: -1.96 ± 1.31			
				Distance: 0.02 ± 0.72			
		18 (11)	Age + Distance	Age: -1.73 ± 0.68	Age	4.90	0.027*
				Distance: 0.15 ± 0.35	Distance	0.17	0.684
		18 (11)	Age	-1.74 ± 0.68	Age	4.99	0.026*
		18 (11)	Distance	0.18 ± 0.36	Distance	0.25	0.618
		21 (12)[a]	Age	-1.68 ± 0.63	Age	5.84	0.016*
	All Sites	31 (18)	Age * Distance	Age:Distance: -0.49 ± 0.40	Interaction	1.53	0.216
				Age: -0.57 ± 0.57			
				Distance: 0.54 ± 0.43			
		31 (18)	Age + Distance	Age: -0.97 ± 0.48	Age	3.80	0.051

				Distance: 0.06 ± 0.21	Distance	0.09	0.759
		31 (18)	Age	-0.98 ± 0.48	Age	3.91	0.048*
		31 (18)	Distance	0.010 ± 0.22	Distance	0.20	0.653
		35 (20)[a]	Age	-0.95 ± 0.44	Age	4.32	0.038*
Relative MNTD	Old World	13 (7)	Age * Distance	Age:Distance: -0.08 ± 0.03	Interaction	4.69	0.030*
				Age: -0.06 ± 0.02			
				Distance: 0.06 ± 0.03			
		13 (7)	Age + Distance	Age: -0.07 ± 0.02	Age	6.48	0.011*
				Distance: -0.01 ± 0.01	Distance	2.04	0.154
		13 (7)	Age	-0.06 ± 0.02	Age	5.91	0.015*
		13 (7)	Distance	-0.01 ± 0.01	Distance	1.47	0.226
		14 (8)[a]	Age	-0.06 ± 0.02	Age	5.87	0.015*
	New World	18 (11)	Age * Distance	Age:Distance: -0.01 ± 0.02	Interaction	0.207	0.649
				Age: 0.02 ± 0.04			
				Distance: 0.01 ± 0.02			
		18 (11)	Age + Distance	Age: 0.00 ± 0.02	Age	0.01	0.942
				Distance: 0.00 ± 0.01	Distance	<0.01	0.962
		18 (11)	Age	0.00 ± 0.02	Age	<0.01	0.951
		18 (11)	Distance	0.00 ± 0.01	Distance	<0.01	0.980
		21 (12)[a]	Age	0.01 ± 0.02	Age	0.06	0.813

	All Sites	31 (18)	Age * Distance	Age:Distance: 0.01 ± 0.01	Interaction	0.57	0.449
				Age: -0.05 ± 0.02			
				Distance: -0.02 ± 0.01			
		31 (18)	Age + Distance	Age: -0.04 ± 0.01	Age	4.90	0.027*
				Distance: -0.01 ± 0.01	Distance	0.74	0.390
		31 (18)	Age	-0.04 ± 0.01	Age	4.66	0.031*
		31 (18)	Distance	-0.01 ± 0.01	Distance	0.50	0.478
		35 (20)[a]	Age	-0.03 ± 0.02	Age	2.91	0.088
Relative ses.MNTD	Old World	13 (7)	Age * Distance	Age:Distance: -0.82 ± 0.62	Interaction	1.64	0.200
				Age: -0.91 ± 0.35			
				Distance: 0.46 ± 0.57			
		13 (7)	Age + Distance	Age: -0.99 ± 0.37	Age	5.66	0.017*
				Distance: -0.28 ± 0.13	Distance	2.63	0.105
		13 (7)	Age	-0.73 ± 0.32	Age	4.39	0.036*
		13 (7)	Distance	-0.25 ± 0.16	Distance	1.35	0.245
		14 (8)[a]	Age	-0.69 ± 0.31	Age	4.08	0.043*
	New World	18 (11)	Age * Distance	Age:Distance: 0.12 ± 0.35	Interaction	0.10	0.750
				Age: -0.05 ± 0.72			
				Distance: -0.15 ± 0.38			
		18 (11)	Age + Distance	Age: 0.21 ± 0.40	Age	0.15	0.702

			Distance: -0.03 ± 0.17	Distance	0.02	0.878
	18 (11)	Age	0.23 ± 0.40	Age	0.17	0.678
	18 (11)	Distance	-0.04 ± 0.18	Distance	0.05	0.824
	21 (12)[a]	Age	0.29 ± 0.39	Age	0.41	0.523
All Sites	31 (18)	Age * Distance	Age:Distance: 0.27 ± 0.21	Interaction	1.62	0.203
			Age: -0.67 ± 0.28			
			Distance: -0.41 ± 0.24			
	31 (18)	Age + Distance	Age: -0.47 ± 0.24	Age	2.87	0.090
			Distance: -0.15 ± 0.14	Distance	1.11	0.291
	31 (18)	Age	-0.46 ± 0.25	Age	2.64	0.104
	31 (18)	Distance	-0.13 ± 0.13	Distance	0.89	0.347
	35 (20)[a]	Age	-0.39 ± 0.25	Age	1.86	0.172

a Model built containing observations from all study sites (i.e. includes those sites without data on distance to primary forest).

Table S7: Models for sites in the Old World, New World and across all sites, constructed for testing the effects of secondary forest age, and distance between paired secondary and primary forest sites, on forest dependent species recovery.

Response	**World Location**	**Observations (Group Size)**	**Model**	**Slope Estimate (± SE)**	**Term dropped in LRT**	**LRT Statistic (χ^2)**	**p-value**
Relative % Forest dependent Species	Old World	13 (7)	Age * Distance	Age:Distance: 11.82 ± 5.09 Age: 7.96 ± 2.92 Distance: -12.26 ± 4.72	Interaction	4.51	0.034*
		13 (7)	Age + Distance	Age: 9.09 ± 3.43 Distance: -1.56 ± 1.17	Age Distance	5.63 1.66	0.018* 0.198
		13 (7)	Age	9.48 ± 3.64	Age	5.46	0.019*
		13 (7)	Distance	-1.82 ± 1.45	Distance	1.49	0.222
		14 (8)[a]	Age	10.21 ± 3.38	Age	7.02	0.008**
	New World	18 (11)	Age * Distance	Age:Distance: -0.70 ± 3.00 Age: 9.26 ± 6.20 Distance: -1.25 ± 3.20	Interaction	0.05	0.816
		18 (11)	Age + Distance	Age: 8.10 ± 3.67	Age	4.31	0.038*

			Distance: -1.94 ± 1.25	Distance	2.26	0.133
	18 (11)	Age	7.91 ± 3.91	Age	3.70	0.055
	18 (11)	Distance	-1.85 ± 1.40	Distance	1.65	0.199
	21 (12)[a]	Age	7.86 ± 3.69	Age	4.12	0.043*
All Sites	31 (18)	Age * Distance	Age:Distance: 0.35 ± 2.15	Interaction	0.03	0.871
			Age: 8.20 ± 3.24			
			Distance: -2.47 ± 2.26			
	31 (18)	Age + Distance	Age: 8.50 ± 2.65	Age	8.88	0.003**
			Distance: -2.13 ± 0.88	Distance	5.08	0.024*
	31 (18)	Age	9.06 ± 2.78	Age	8.20	0.004**
	31 (18)	Distance	-2.20 ± 1.01	Distance	4.40	0.036*
	35 (20)[a]	Age	9.68 ± 2.69	Age	9.55	0.002**

a Model built containing observations from all study sites (i.e. includes those sites without data on distance to primary forest).

Table S8: Models for sites in the Old World, New World and across all sites, constructed for testing the effects of elevation, precipitation and temperature between paired secondary and primary forest sites, on the response variables listed. Models contained each single predictor variable (elevation, precipitation and temperature) alone, and combined with the predictor variables (age, distance) from the most well supported model identified in the main analysis.

Response	**World Location**	**Observations (Group Size)**	**Model**	**Slope Estimate (± SE) for Term Dropped in LRT**	**Term Dropped in LRT**	**LRT Statistic (χ^2)**	**p-value**
ßTD	Old World	13 (7)	Age * Distance + Elevation	0.03 ± 0.04	Elevation	0.60	0.441
		13 (7)	Age * Distance + Precipitation	-0.17 ± 0.26	Precipitation	0.43	0.511
		13 (7)	Age * Distance + Temperature	-0.51 ± 0.43	Temperature	1.37	0.242
		14 (8)[a]	Elevation	0.03 ± 0.08	Elevation	0.11	0.741
		14 (8)[a]	Precipitation	-0.45 ± 0.33	Precipitation	1.80	0.180
		14 (8)[a]	Temperature	-0.21 ± 0.86	Temperature	0.06	0.806
	New World	18 (11)	Distance + Elevation	0.00 ± 0.03	Elevation	0.01	0.937
		18 (11)	Distance + Precipitation	-0.08 ± 0.09	Precipitation	0.77	0.380
		18 (11)	Distance + Temperature	-0.55 ± 0.41	Temperature	1.67	0.197
		21 (12)[a]	Elevation	-0.01 ± 0.04	Elevation	0.14	0.711
		21 (12)[a]	Precipitation	-0.04 ± 0.12	Precipitation	0.11	0.745
		21 (12)[a]	Temperature	-0.07 ± 0.39	Temperature	0.03	0.859
	All Sites	31 (18)	Age + Elevation	0.01 ± 0.05	Elevation	0.06	0.799

		31 (18)	Age + Precipitation	0.06 ± 0.13	Precipitation	0.20	0.652
		31 (18)	Age + Temperature	-0.58 ± 0.46	Temperature	1.42	0.233
		35 (20)[a]	Elevation	-0.01 ± 0.04	Elevation	0.03	0.864
		35 (20)[a]	Precipitation	-0.11 ± 0.12	Precipitation	0.79	0.373
		35 (20)[a]	Temperature	-0.11 ± 0.37	Temperature	0.09	0.767
ßPD	Old World	13 (7)	Age * Distance + Elevation	0.01 ± 0.03	Elevation	0.04	0.851
		13 (7)	Age * Distance + Precipitation	-0.06 ± 0.21	Precipitation	0.07	0.785
		13 (7)	Age * Distance + Temperature	-0.22 ± 0.35	Temperature	0.40	0.525
		14 (8)[a]	Elevation	0.01 ± 0.07	Elevation	0.01	0.904
		14 (8)[a]	Precipitation	-0.38 ± 0.29	Precipitation	1.64	0.200
		14 (8)[a]	Temperature	-0.04 ± 0.76	Temperature	<0.01	0.961
	New World	21 (12)[a]	Elevation	-0.01 ± 0.03	Elevation	0.09	0.762
		21 (12)[a]	Precipitation	-0.00 ± 0.10	Precipitation	<0.01	0.980
		21 (12)[a]	Temperature	0.03 ± 0.31	Temperature	<0.01	0.935
	All Sites	31 (18)	Age + Elevation	-0.00 ± 0.04	Elevation	<0.01	1.000
		31 (18)	Age + Precipitation	0.05 ± 0.10	Precipitation	0.25	0.620
		31 (18)	Age + Temperature	-0.34 ± 0.34	Temperature	0.87	0.351
		35 (20)[a]	Elevation	-0.01 ± 0.03	Elevation	0.03	0.857
		35 (20)[a]	Precipitation	-0.06 ± 0.10	Precipitation	0.34	0.558
		35 (20)[a]	Temperature	0.01 ± 0.31	Temperature	<0.01	0.975

Relative SR	Old World	13 (7)	Age * Distance + Elevation	0.07 ± 0.04	Elevation	3.29	0.070
		13 (7)	Age * Distance + Precipitation	-0.45 ± 0.27	Precipitation	2.52	0.112
		13 (7)	Age * Distance + Temperature	-0.77 ± 0.45	Temperature	2.63	0.105
		14 (8)[a]	Elevation	0.07 ± 0.05	Elevation	1.70	0.193
		14 (8)[a]	Precipitation	-0.51 ± 0.21	Precipitation	4.87	0.027*
		14 (8)[a]	Temperature	-0.62 ± 0.60	Temperature	1.02	0.312
	New World	21 (12)[a]	Elevation	-0.07 ± 0.04	Elevation	2.15	0.142
		21 (12)[a]	Precipitation	-0.08 ± 0.14	Precipitation	0.35	0.556
		21 (12)[a]	Temperature	0.73 ± 0.38	Temperature	2.11	0.146
	All Sites	35 (20)[a]	Elevation	-0.03 ± 0.03	Elevation	0.64	0.425
		35 (20)[a]	Precipitation	-0.15 ± 0.11	Precipitation	1.65	0.199
		35 (20)[a]	Temperature	0.46 ± 0.33	Temperature	1.35	0.246
Relative PD	Old World	14 (8)[a]	Age + Elevation	0.05 ± 0.04	Elevation	1.56	0.212
		14 (8)[a]	Age + Precipitation	-0.30 ± 0.16	Precipitation	3.11	0.078
		14 (8)[a]	Age + Temperature	-0.40 ± 0.43	Temperature	0.82	0.367
		14 (8)[a]	Elevation	0.04 ± 0.05	Elevation	0.86	0.353
		14 (8)[a]	Precipitation	-0.35 ± 0.18	Precipitation	3.32	0.069
		14 (8)[a]	Temperature	-0.32 ± 0.51	Temperature	0.40	0.526
	New World	21 (12)[a]	Elevation	-0.06 ± 0.04	Elevation	2.25	0.134

		21 (12)[a]	Precipitation	-0.04 ± 0.11	Precipitation	0.13	0.715
		21 (12)[a]	Temperature	0.73 ± 0.31	Temperature	2.80	0.094
	All Sites	35 (20)[a]	Elevation	-0.03 ± 0.03	Elevation	0.88	0.348
		35 (20)[a]	Precipitation	-0.09 ± 0.10	Precipitation	0.87	0.350
		35 (20)[a]	Temperature	0.54 ± 0.27	Temperature	2.37	0.123
Relative ses.PD	Old World	14 (8)[a]	Elevation	-0.39 ± 0.58	Elevation	0.45	0.504
		14 (8)[a]	Precipitation	1.62 ± 2.53	Precipitation	0.40	0.526
		14 (8)[a]	Temperature	3.51 ± 6.33	Temperature	0.30	0.582
	New World	21 (12)[a]	Elevation	0.13 ± 0.41	Elevation	0.10	0.756
		21 (12)[a]	Precipitation	0.58 ± 1.03	Precipitation	0.31	0.577
		21 (12)[a]	Temperature	-0.63 ± 3.75	Temperature	0.03	0.868
	All Sites	35 (20)[a]	Elevation	-0.04 ± 0.33	Elevation	0.01	0.905
		35 (20)[a]	Precipitation	0.98 ± 0.95	Precipitation	0.91	0.339
		35 (20)[a]	Temperature	0.92 ± 3.21	Temperature	0.08	0.777
Relative MPD	Old World	14 (8)[a]	Elevation	-0.01 ± 0.01	Elevation	1.00	0.316
		14 (8)[a]	Precipitation	0.04 ± 0.05	Precipitation	0.68	0.411
		14 (8)[a]	Temperature	0.21 ± 0.11	Temperature	3.07	0.080
	New World	21 (12)[a]	Elevation	-0.01 ± 0.01	Elevation	1.49	0.222
		21 (12)[a]	Precipitation	0.03 ± 0.03	Precipitation	1.27	0.259
		21 (12)[a]	Temperature	0.16 ± 0.09	Temperature	2.76	0.097

	All Sites	35 (20)[a]	Elevation	-0.01 ± 0.01	Elevation	2.19	0.139
		35 (20)[a]	Precipitation	0.03 ± 0.02	Precipitation	1.61	0.205
		35 (20)[a]	Temperature	0.19 ± 0.07	Temperature	5.37	0.021*
Relative ses.MPD	Old World	14 (8)[a]	Elevation	-0.28 ± 0.62	Elevation	0.20	0.655
		14 (8)[a]	Precipitation	2.23 ± 2.67	Precipitation	0.68	0.410
		14 (8)[a]	Temperature	6.61 ± 6.59	Temperature	0.97	0.324
	New World	21 (12)[a]	Age + Elevation	-0.27 ± 0.62	Elevation	0.19	0.666
		21 (12)[a]	Age + Precipitation	1.49 ± 1.54	Precipitation	0.89	0.345
		21 (12)[a]	Age + Temperature	4.44 ± 5.51	Temperature	0.62	0.431
		21 (12)[a]	Elevation	-0.54 ± 0.65	Elevation	0.65	0.419
		21 (12)[a]	Precipitation	2.20 ± 1.58	Precipitation	1.80	0.180
		21 (12)[a]	Temperature	6.78 ± 5.66	Temperature	1.30	0.255
	All Sites	35 (20)[a]	Elevation	-0.49 ± 0.47	Elevation	1.03	0.309
		35 (20)[a]	Precipitation	2.29 ± 1.34	Precipitation	2.69	0.101
		35 (20)[a]	Temperature	8.16 ± 4.22	Temperature	3.02	0.082
Relative MNTD	Old World	13 (7)	Age + Elevation	-0.05 ± 0.03	Elevation	1.76	0.184
		13 (7)	Age + Precipitation	0.21 ± 0.13	Precipitation	2.15	0.143
		13 (7)	Age + Temperature	0.35 ± 0.35	Temperature	0.90	0.343
		14 (8)[a]	Elevation	-0.04 ± 0.03	Elevation	1.23	0.267
		14 (8)[a]	Precipitation	0.22 ± 0.13	Precipitation	2.63	0.105

		14 (8)[a]	Temperature	0.33 ± 0.35	Temperature	0.85	0.357
	New World	21 (12)[a]	Elevation	0.00 ± 0.02	Elevation	0.02	0.888
		21 (12)[a]	Precipitation	0.04 ± 0.04	Precipitation	0.57	0.452
		21 (12)[a]	Temperature	0.13 ± 0.14	Temperature	0.66	0.417
	All Sites	35 (20)[a]	Elevation	-0.01 ± 0.01	Elevation	0.27	0.604
		35 (20)[a]	Precipitation	0.07 ± 0.05	Precipitation	2.04	0.153
		35 (20)[a]	Temperature	0.18 ± 0.14	Temperature	1.50	0.221
Relative ses.MNTD	Old World	14 (8)[a]	Elevation	-0.24 ± 0.63	Elevation	0.14	0.705
		14 (8)[a]	Precipitation	1.42 ± 2.62	Precipitation	0.29	0.591
		14 (8)[a]	Temperature	1.50 ± 7.31	Temperature	0.04	0.838
	New World	21 (12)[a]	Elevation	0.13 ± 0.30	Elevation	0.18	0.670
		21 (12)[a]	Precipitation	0.19 ± 0.79	Precipitation	0.06	0.812
		21 (12)[a]	Temperature	-0.37 ± 2.79	Temperature	0.02	0.897
	All Sites	35 (20)[a]	Elevation	0.01 ± 0.30	Elevation	<0.01	0.984
		35 (20)[a]	Precipitation	0.40 ± 0.89	Precipitation	0.197	0.658
		35 (20)[a]	Temperature	0.19 ± 2.97	Temperature	<0.01	0.949
Relative % Forest Dependent Species	Old World	13 (7)	Age * Distance + Elevation	-1.54 ± 2.85	Elevation	0.29	0.592
		13 (7)	Age * Distance + Precipitation	12.66 ± 20.74	Precipitation	0.34	0.545
		13 (7)	Age * Distance + Temperature	2.04 ± 35.43	Temperature	<0.01	0.954
		14 (8)[a]	Elevation	-0.36 ± 4.35	Elevation	0.01	0.935

		14 (8)[a]	Precipitation	-29.59 ± 17.24	Precipitation	2.67	0.102
		14 (8)[a]	Temperature	-34.85 ± 46.39	Temperature	0.55	0.457
	New World	18 (11)	Age + Elevation	2.75 ± 2.11	Elevation	1.63	0.202
		18 (11)	Age + Precipitation	-0.92 ± 6.85	Precipitation	0.02	0.893
		18 (11)	Age + Temperature	-74.17 ± 22.57	Temperature	8.46	0.004**
		21 (12)[a]	Elevation	3.15 ± 2.18	Elevation	1.98	0.159
		21 (12)[a]	Precipitation	-4.40 ± 7.22	Precipitation	0.37	0.545
		21 (12)[a]	Temperature	-43.23 ± 21.15	Temperature	3.81	0.051
	All Sites	31 (18)	Age + Distance + Elevation	1.75 ± 1.79	Elevation	0.95	0.331
		31 (18)	Age + Distance + Precipitation	-4.65 ± 6.00	Precipitation	0.59	0.441
		31 (18)	Age + Distance + Temperature	-56.30 ± 21.61	Temperature	6.14	0.013*
		35 (20)[a]	Elevation	1.938 ± 2.181	Elevation	0.78	0.377
		35 (20)[a]	Precipitation	-9.494 ± 7.279	Precipitation	1.66	0.197
		35 (20)[a]	Temperature	-42.96 ± 21.54	Temperature	3.77	0.052

a Model built containing observations from all study sites (i.e. includes those sites without data on distance to primary forest).

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LETTER

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Global biogeographic patterns of avian morphological diversity

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Abstract

Understanding the biogeographical patterns, and evolutionary and environmental drivers, underpinning morphological diversity are key for determining its origins and conservation. Using a comprehensive set of continuous morphological traits extracted from museum collections of 8353 bird species, including geometric morphometric beak shape data, we find that avian morphological diversity is unevenly distributed globally, even after controlling for species richness, with exceptionally dense packing of species in hyper-diverse tropical hotspots. At the regional level, these areas also have high morphological variance, with species exhibiting high phenotypic diversity. Evolutionary history likely plays a key role in shaping these patterns, with evolutionarily old species contributing to niche expansion, and young species contributing to niche packing. Taken together, these results imply that the tropics are both 'cradles' and 'museums' of phenotypic diversity.

KEYWORDS
avian biodiversity, community structure, morphological diversity, morphological traits, morphospace, niche expansion, niche packing

INTRODUCTION

Exploring and understanding global patterns of biodiversity is central for determining its origins and conservation. Numerous hypotheses have been posited to explain how biodiversity has accumulated over geographical space and evolutionary time, with particular focus on how species richness varies across major environmental gradients (Currie et al., 1999; Gaston, 2000; MacArthur, 1965; Rohde, 1992). However, species richness-based metrics of diversity consider all species as equal units, ignoring differences among species in their evolutionary history, morphology or ecological roles, and do not adequately explain community structure or the mechanisms underlying species coexistence (Devictor et al., 2010; Faith, 1992; Purvis & Hector, 2000; Safi et al., 2011; Stevens et al., 2003). One approach to combating these shortfalls is to classify species according to their functional roles (e.g. diet, behaviour or life history), allowing investigation into how species are structured within communities, and the potential historical, environmental and ecological drivers leading to spatial variation in community assembly (Belmaker et al., 2012; Safi et al., 2011).

An alternative to classifying species into functional groups based on scoring of functional roles is to use continuous morphological traits to capture ecologically relevant variation (Jones et al., 2009; Kohli & Jarzyna, 2021; McLean et al., 2021; Oliveira et al., 2017; Pigot et al., 2020; Pigot, Trisos, et al., 2016; Wilman et al., 2014). This is beneficial where behavioural observations are lacking or unavailable for rare or cryptic species, across large geographical scales and for whole taxonomic groups. More generally, recent simulation studies have shown

that using coarse grained data can be misleading in studies of species community or assemblage structure and recommend the use of high-resolution continuous data where possible (Kohli & Jarzyna, 2021). Such detailed morphological trait data can capture variation among functional categories (Pigot et al., 2020), providing fine-grained resolution that distinguishes multiple morphologies filling a single functional role and avoids the need to assign species to functional categories. The advent of novel, high-quality datasets of morphological traits for entire classes has advanced understanding of how communities fill multidimensional trait space (i.e. morphospace) (Pigot, Trisos, et al., 2016), how morphological form maps to ecological role and/ or function (Anderson et al., 2011; Bright et al., 2016, 2019; Miller et al., 2017; Navalón et al., 2019; Olsen, 2017; Pigot et al., 2020), and how morphological diversity has evolved and is distributed across the phylogeny (Cooney et al., 2017). Nonetheless, with a few exceptions (McLean et al., 2021; Sheard et al., 2020), we lack good understanding of the biogeographical patterns of morphological diversity at a global scale, and thus of the macroecological factors driving trait diversity both within and across species assemblages. In this study, we use continuously measured morphological traits as a high-resolution approximation of the diversity of ecological roles.

Communities vary in terms of their species richness, and this variation may be associated with ecological 'niche packing' and/or 'niche expansion' (Karr & James, 1975; MacArthur, 1965; Pigot, Trisos, et al., 2016). The packing of niche space occurs because of the finer specialisation of phenotypes or increased overlap in resource use, leading to increased density of species in morphospace over a smaller volume (Karr & James, 1975; MacArthur, 1965; Pigot, Trisos, et al., 2016). Alternatively, species may fill an expanded variety of niches and exhibit dissimilar morphologies, revealed by higher volumes and lower densities of species in morphospace (Pigot, Trisos, et al., 2016). Investigating how species fill morphospace in terms of both the volume and density occupied can therefore inform on the species richness of communities.

Variation in communities' morphological diversity results from a combination of evolutionary and environmental factors that have shaped global patterns of biodiversity accumulation (Safi et al., 2011), leading to the prediction that avian morphological diversity will be distributed unevenly across the globe. For instance, in heterogeneous habitats, species are likely to coexist because of greater availability of niches (Guégan et al., 1998; Kerr & Packer, 1997; Kerr et al., 2001; MacArthur & MacArthur, 1961; Rahbek & Graves, 2001), and we therefore predict that assemblages will occupy morphospace at higher density than in homogeneous habitats. Habitats are also expected to vary with altitude (Davies et al., 2007; Kerr & Packer, 1997; Rahbek & Graves, 2001), with mountainous regions forming important dispersal barriers, centres for recent speciation, and exhibiting high species richness (α-diversity) and turnover (β-diversity) across entire montane slopes (Davies et al., 2007; Graham et al., 2009; Jarzyna et al., 2021; Melo et al., 2009; Voskamp et al., 2017). We expect to find high morphological density, with species filling similar areas in trait space, in areas transcending the largest altitudinal ranges (i.e. mid-montane slopes) because of the packing of niche space of closely related species, both before, and after controlling for species richness.

The influence of ecological limits to species coexistence may be reduced in areas of high productivity as resources are plentiful (Mittelbach et al., 2001; Pigot, Tobias, et al., 2016), potentially supporting many species filling similar roles (i.e. niche packing) that are more finely specialised in their morphology. Equally, if resources are limited, communities may show low morphological density, with species needing to occupy wider ecological niches (Safi et al., 2011). Consequently, we predict the greatest morphological density in highly productive areas, and low morphological density where productivity is poor.

Evolutionary factors also influence the temporal accumulation of biodiversity. Over time, the divergence of species and their traits will shape the accumulation of phenotypic diversity in communities. Species that represent older, more isolated branches – that is, those with higher evolutionary distinctness (Jetz et al., 2014; Redding & Mooers, 2006; Vane-Wright et al., 1991) – may possess phenotypic traits that are unique and so fill otherwise unoccupied areas of trait space (Jetz et al., 2014; Redding et al., 2010). We predict that assemblages with high sums of evolutionary distinctiveness, and therefore representing more total evolutionary history, will have greater phenotypic diversity. These assemblages should contain species that are spread out in morphospace, leading to higher morphological volumes and lower morphological densities.

Here, we focus on testing these predictions in birds, which exhibit a huge diversity of phenotypes (Cooney et al., 2017; Pigot et al., 2020; Tobias et al., 2020), worldwide distribution across all terrestrial land-masses (Orme et al., 2005), and high-quality phylogenetic and trait data (Cooney et al., 2017; Jetz et al., 2012; Wilman et al., 2014). We use ecologically relevant morphological traits to: (1) map global patterns of avian morphological diversity; (2) identify areas with exceptional levels of morphological diversity; and (3) test the environmental and evolutionary drivers of global avian morphological diversity.

MATERIALS AND METHODS

All data compilation, analysis and visualisation were conducted in RStudio version 1.3.959 (RStudio Team, 2020) and R version 4.0.2 (R Core Team, 2020). We follow

the taxonomy used in the BirdTree phylogeny http://birdtree.org/ (Jetz et al., 2012).

Morphological trait data

We compiled a dataset of continuous morphological traits that are linked to the ecological niches of birds in a community (Pigot, Trisos, et al., 2016; Sheard et al., 2020).

Trait compilation

Using a 3D landmark-based beak shape dataset, we extracted coordinates for the bill shape for 8353 species of bird, across 189 (of 194) bird families. 3D scanning, post processing and landmarking were performed using protocols described in Chira et al. (2018) and Cooney et al. (2017). In summary, we took 3D scans of the beaks of museum study skins, using white and blue structured light scanning (*FlexScan3D*). For some families (e.g. nightjars [Caprimulgidae]), many species could not be scanned as they had feathers and/or bristles obscuring parts of the beak, and are therefore underrepresented in our dataset (Figure S1). From these scans, we used landmark-based geometric morphometric analysis to measure bill shape and ran a principal component analysis (PCA) to produce a morphospace capturing the major axes of bill shape variation (see Supplementary Material S1a for further information).

We extracted the first seven axes from the PCA, which accounted for 98.9% of the overall variation in bill shape (Figure S2, Table S1). We calculated centroid size as a measure of bill size for each species in our dataset. For each specimen scanned, we took measurements of wing and tarsus length (mm). Where possible, if these measurements were not taken (e.g. broken tarsus or sewn wings), another specimen or a mean score calculated from multiple specimens was used. Body mass (g) for each species was taken from the EltonTraits database (Wilman et al., 2014). We include centroid size as well as body size because there is substantial variation in beak size that cannot be explained by allometry alone (e.g. raptors, Bright et al., 2016).

Avian morphological trait space

Next, we constructed a raw morphological trait dataset containing the seven main axes of beak shape variation, and combined them with $\log_{10}$-transformed measurements of body mass, centroid size, wing and tarsus length. Trait data were centred and re-scaled by standardising each to zero mean and unit variance (z-transformation). Finally, we ran a second PCA on this combined dataset and selected the first eight PC axes from the resultant morphospace which represented 96.1% of the variation in traits (Figure 1; Table S1).

Spatial data

Global distribution maps for all extant and probably extant bird species were obtained from BirdLife International (http://www.birdlife.org/datazone/home). Species breeding and resident range maps were included where these species were classified as native or re-introduced. Whilst these maps may be less accurate and do not incorporate abundance data as more focused surveys, they allow for a much broader scope, and analysis in regions where survey data are not available or sufficiently plentiful. As a result of taxonomic differences, we first matched species names used by BirdLife to the BirdTree phylogeny http://birdtree.org/ (Jetz et al., 2012), and range maps were projected onto a 100 km x 100 km equal area grid under a Behrmann cylindrical equal-area projection (see Supplementary Material S1b for further detail). Species presence or absence in each terrestrial grid cell was recorded. Our final dataset comprised 8353/9993 (83.6%) species, distributed across 15980 assemblages. For each assemblage, species lists and species richness were obtained. Global maps and phylogenetic plots of omitted species can be found in Figures S1 and S3.

Morphological disparity metrics

Numerous disparity metrics have been proposed to assess how species occupy multidimensional trait space. Using single metrics to quantify multidimensional space occupancy limits the ecological inferences that can be made (Guillerme et al., 2020; Villéger et al., 2008). Therefore, we aimed to select one metric that accurately captured changes in morphospace volume and another that captured changes in density (i.e. how species fill trait space).

To quantify and understand the potential for different metrics to capture such changes in volume and density, we used the function *test.metric* in the R package *dispRity* (version 1.5.0: Guillerme, 2018), following protocols described by Guillerme et al. (2020). Based on simulations of species gains and loss, we selected the metrics (i) sum of variance (Foote, 1992), and (ii) mean distance to nearest neighbour (i.e. the mean Euclidean distance between a species and its nearest neighbour: Foote, 1992). The sum of variance is commonly used as a measure of volume, but it may also capture certain aspects of density (Guillerme et al., 2020) (e.g. a high number of species close to the mean trait value will reduce the sum of variance). Therefore, we define the sum of variance as a measure that captures the spread, or variance, of species in trait space (morphological variance). We decided against using a commonly used, alternative measure of volume, the sum of ranges (Foote, 1992), as it is more sensitive to

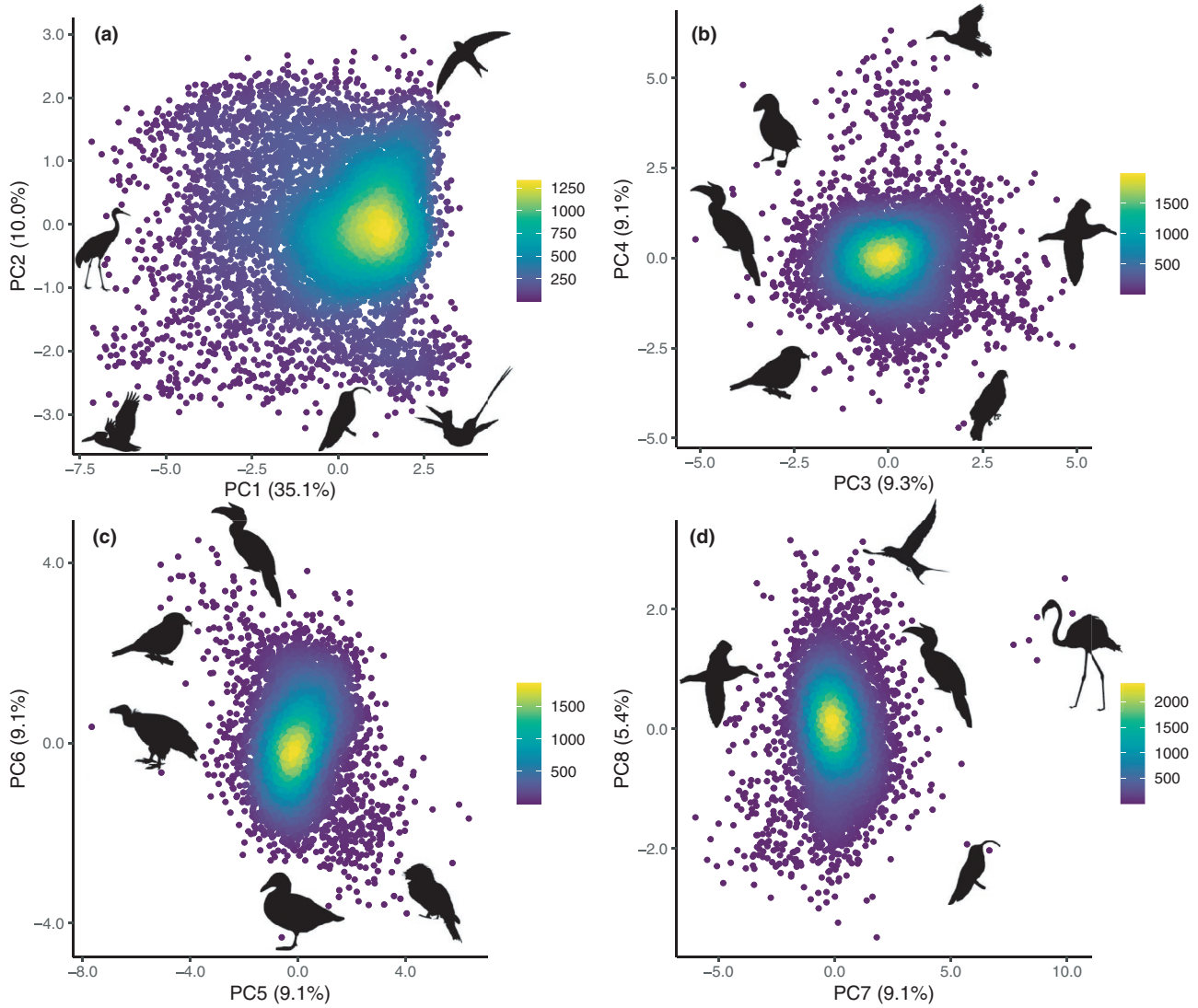

FIGURE 1 Scatterplots showing the first eight principal components of morphological traits, and the proportion of variance represented by each. The scale bar shows the number of neighbouring points within one standard deviation of the Euclidean distance of each species to all other species across both axes for each scatterplot. Points were coloured with yellow being where species are most numerous, and purple least numerous. PC1 is dominated by size metrics, with high values corresponding to small body mass, tarsus, wing and bill (centroid) size, and the largest species falling at negative values. PC2 captures the main variation of beak shape, going from long, pointy bills at the negative end of the spectrum, to wide, short bills at the positive end. The remaining PCs capture more nuanced variation in beak shape (Figure S2). All silhouettes are in the public domain, and were downloaded from PhyloPic.org.

outliers (Guillerme et al., 2020). The mean distance to nearest neighbour quantifies the density of species packing in morphospace (morphological density). Both metrics were calculated for each unique assemblage using the *dispRity* R package (version 1.5.0: Guillerme, 2018).

Assemblage evolutionary distinctiveness

We downloaded 100 complete species-level phylogenetic trees based on the Hackett backbone (Hackett et al., 2008) from http://birdtree.org/ (Jetz et al., 2012). For each tree, we calculated an evolutionary distinctiveness score for each species in the phylogeny (n = 9993), using the 'equal splits' derivation (Redding & Mooers, 2006) in the *evol.distinct* function in the R package *picante* (version 1.8.2: Kembel et al., 2010). 'Equal splits' divides each branch length by the daughter species it represents, giving a value for each species of the amount of evolutionary time each embodies. For each community, evolutionary distinctiveness scores for all species present were summed. This was done for each of the 100 trees, and a mean value was taken giving an 'assemblage evolutionary distinctiveness' score for each community.

Null models

To test whether the morphological variance, density and assemblage evolutionary distinctiveness of each

assemblage deviated from expected given the observed species richness, we constructed null models based on two different species pools. Firstly, we used a global species pool where any species from the entire dataset could be drawn. Secondly, we used a species pool where draws were restricted to phylogenetically distinct regional pools in order to avoid sampling from largely historically independent assemblages (Figure S4). To do this, we followed the protocol outlined by Holt et al. (2013) and defined 13 unique phylogenetic regions that have distinct evolutionary histories (Section S1c). Null models for each grid cell were calculated using both species pools, enabling us to capture regional effects under a global species pool, and more local effects when using a phyloregional species pool.

For each unique species richness value, 1000 null communities were generated and morphological variance and density were calculated. For each of the 100 sets of evolutionary distinctiveness scores, 1000 null communities were generated, and assemblage evolutionary distinctiveness was calculated. To assess the difference between the observed (variance, density, assemblage evolutionary distinctiveness) and simulated (null) biodiversity values, we calculated the standardised effect size (SES) for each assemblage: A positive SES value indicates a higher biodiversity value than expected based on null simulations, while a negative SES indicates a lower value. Exceptional values of morphological variance, density and assemblage evolutionary distinctiveness were those that showed statistically significant deviation from expected (+/− 2).

Environmental correlates

For each grid cell, we extracted environmental variables that we predicted are associated with geographical variation in morphological diversity: main habitat type (Buchhorn et al., 2020), the number of unique habitats (Shannon's index) (Buchhorn et al., 2020), altitudinal range (Fick & Hijmans, 2017) and gross primary productivity (GPP) (Zhang et al., 2017) (see Section S1d for full details).

Predicting patterns of morphological diversity

We fitted generalised least squares (GLS) models using the function *gls* in the R package *nlme* (version 3.1–149: Pinheiro et al., 2020) with either morphological variance$_{SES}$ or morphological density$_{SES}$ (calculated using both global and phyloregional species pools) as response variables. Species richness, assemblage evolutionary distinctiveness$_{SES}$, GPP, habitat heterogeneity, altitudinal range and habitat type were included in the full model as predictor variables, with additional models fitted where the categorical variable habitat type was dropped or included alone (Table S2).

We $\log_{10}$-transformed the variables species richness, GPP, habitat heterogeneity and altitudinal range. To allow for non-linear relationships between our response and predictor variables, we included both linear and quadratic terms of the numeric predictor variables in our models. To account for spatial autocorrelation, all models were fitted with either exponential, gaussian or spherical correlation structures, using spatial information from longitudinal and latitudinal cell centroid values. We used Akaike Information Criterion scores (AIC) to select the best-fitting models for each dependent variable, with the models with the lowest AIC scores considered to be most well-supported (Table S2). Due to computational limits, the 15,277 terrestrial grid cells were split into 25% subsets using a chequerboard approach, where every fourth terrestrial grid cell was included (e.g. set A: 1,5,9… etc.). All models were run on each of the four subsets (Table S2).

RESULTS

Avian morphospace

Variation in avian morphological traits is distributed such that the majority of species occupy a dense core in the centre, with more extreme forms found towards the edges of morphospace (Figure 1; Figure S2) (Chira et al., 2018; Pigot et al., 2020). When considering all morphological traits together, 96% of the variation is captured by 8 PCs (Figure 1). PC1 (35% variation) is dominated by size metrics, describing the spectrum from the largest (e.g. cranes [Gruidae]) to smallest (e.g. hummingbirds [Trochilidae]) species.

The major axis of beak shape primarily loads onto the second PC of morphological trait variation, with long pointed bills (e.g. sword-billed hummingbird [*Ensifera ensifera*]) to short, wide beaks (e.g. swifts [Apodidae]). Certain groups of species occupy distinct areas of morphospace that are only apparent on PC axes that themselves account for low total variation, such as waterfowl (Anseriformes) on PCs 5 and 6, and flamingos (Phoenicopteriformes) on PC7 and PC8.

Global distributions of morphological diversity

Avian morphological diversity is unevenly distributed globally (Figure 2). New Zealand, Patagonia and the Atacama Desert contain assemblages with high values of morphological variance, where species occupy large areas of trait space. Low values of morphological variance are found along the species-rich mountain ranges of the Himalayas and Andes, and the species-impoverished Sahara and Arabian Peninsula (Figure 2a). Areas around the Sahara and Arctic contain communities where nearest neighbour

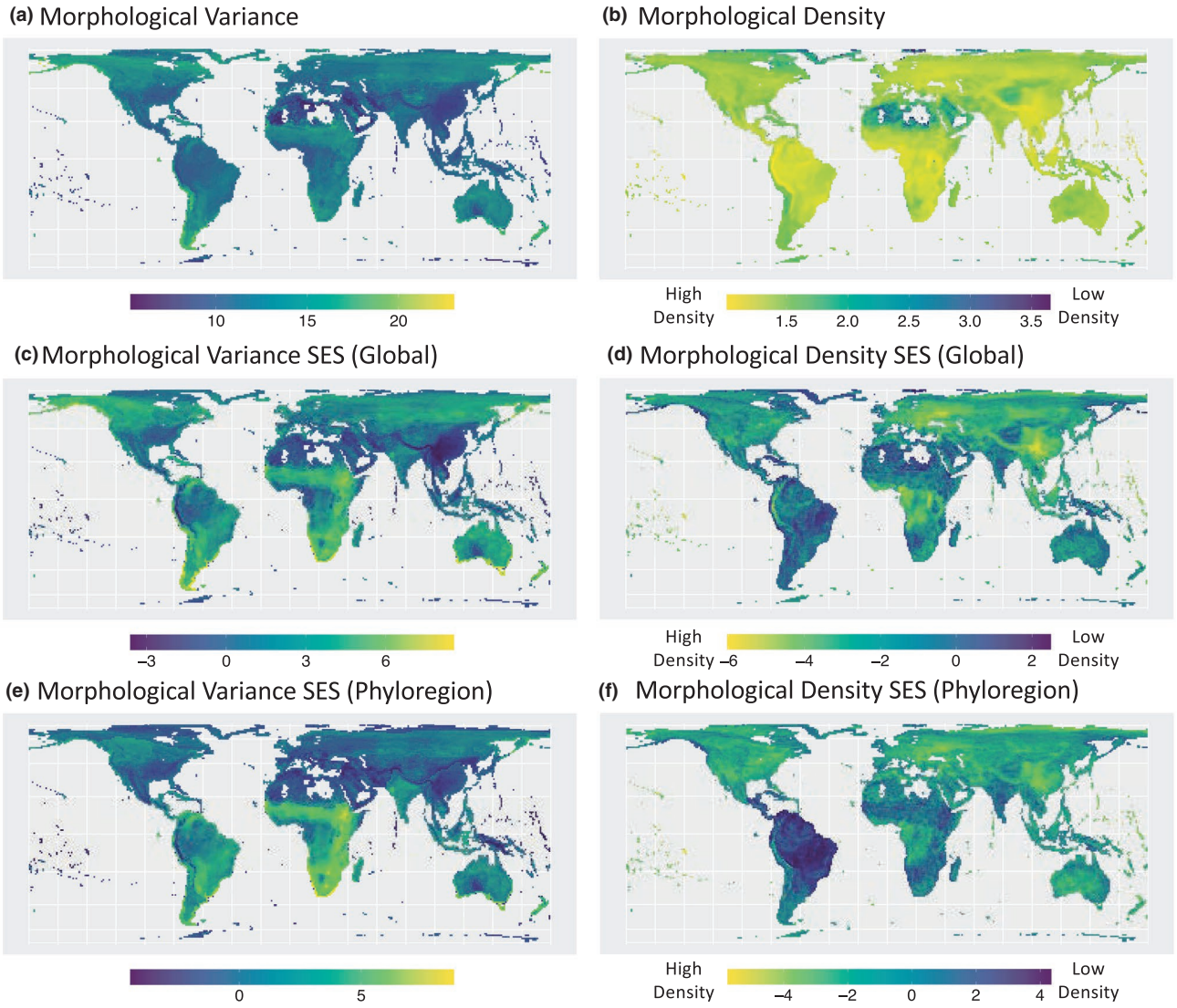

FIGURE 2 (a) Morphological variance (sum of variances) and (b) morphological density (mean nearest neighbour distance) for 8352 bird species across 15980 terrestrial 1 degree grid cells under Behrmann projection. Standard effect sizes (SES) for each variable were calculated from global (c,d) and phyloregional (e,f) species pools.

distance is high, suggesting low morphospace density. Assemblages containing species that are particularly clustered in morphospace (high morphospace density) are found along the Andean and Himalayan mountains, African rift valley and some oceanic islands (Figure 2b).

Communities with the highest assemblage evolutionary distinctiveness are found in the Neotropics, particularly along the Andes and Amazonian basin, African Rift Valley and Himalayas. Low assemblage evolutionary distinctiveness occurs across the Saharo-Arabian belt, polar regions and island archipelagos (Figure S5b). Overall, spatial patterns of the raw metrics suggest a relationship with species richness (Figure 3; Figures S5a and S6) with, for example, the lowest morphological densities occurring in areas of low species richness (Figure 2b) and the highest assemblage evolutionary distinctiveness communities being those with high species richness (Figure S5b).

Geographic distribution of exceptional morphological diversity

Observed morphological variance tends to be greater than expected (Figure 3a) for both global, and to a lesser extent for phyloregional pools (Figure S7). These deviations from expectation show strong spatial patterns. We find higher than expected morphological variance along the South American and South Australian coastlines, and in East and South Africa, when using both global and phyloregional pools, highlighting wider assemblage niche breadths (Figure 2c,e). Differences between the species pools arise in the mountains of New Guinea, where

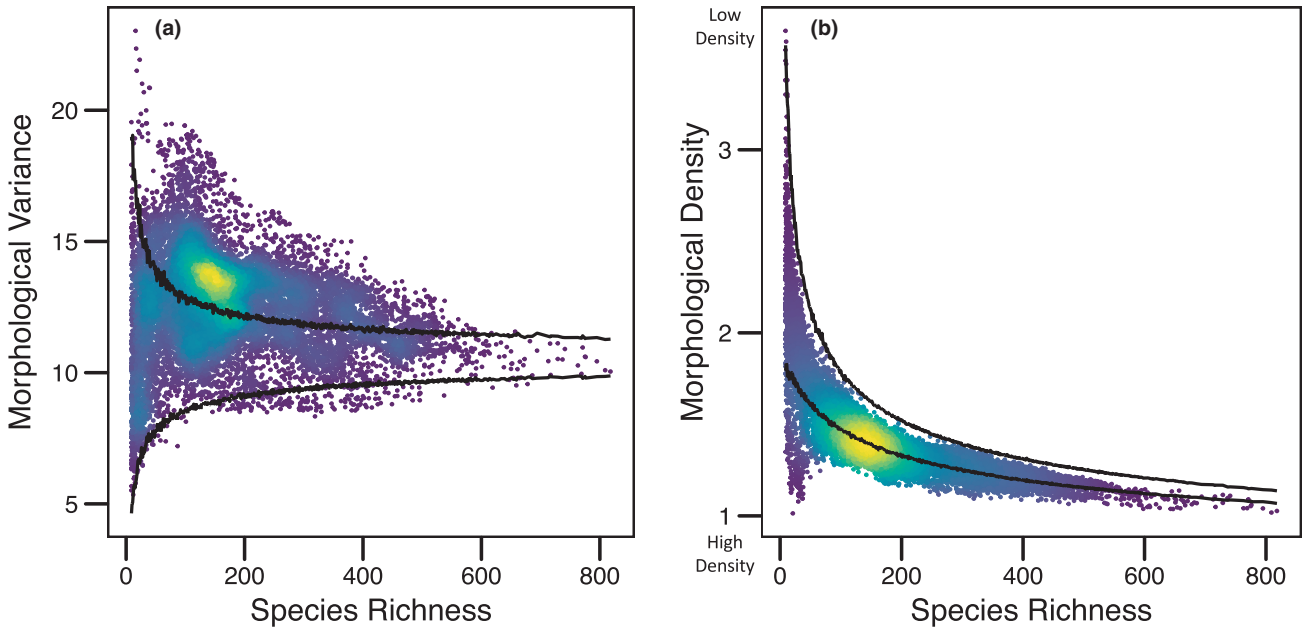

FIGURE 3 Scatter plots showing the relationship between species richness and (a) morphological variance (sum of variances), and (b) morphological density (mean nearest neighbour distance). Points are coloured according to the number of neighbouring points present to highlight where species are most numerous, with yellow the most and purple the least numerous. The lines show the upper (97.5) and lower (2.5) quantiles calculated across null communities drawn from a global species pool for each value of species richness.

morphological variance is much lower than expected using a phyloregional pool, but not a global pool (Figure 2c,e).

Morphological density tends to be greater than expected under a global pool (Figure 3b), but similar to expected when using phyloregional pools (Figure S8). Spatially, we find that for both global and phyloregional species pools, the Andes harbour morphologically dense communities, with species that are more clustered in trait space than expected given species richness (Figure 2d,f). Under a global pool, species occupy morphospace less densely than expected across small areas of the South American lowland tropics, with this pattern extending over greater areas under a phyloregional pool (Figure 2d,f).

We find slightly lower than expected values of assemblage evolutionary distinctiveness for both global and phyloregional null models (Figures S5c,d, S6 and S9). Under a global species pool, assemblages in the tropics and Southern Hemisphere are more evolutionarily distinct than expected based on null simulations, with hotspots in Madagascar, Borneo, tropical central Africa, etc. (Figure S5c). The Andes contain much lower assemblage evolutionary distinctiveness than expected, with younger lineages and/or close relatives dominating (Figure S5c). Patterns are similar under phyloregional pools, but with Australasian assemblages showing expected, rather than greater, assemblage evolutionary distinctiveness (Figure S5d).

We identified areas with combinations of exceptional (+/− 2 s.d) morphological variance, morphological density or assemblage evolutionary distinctiveness. Using global species pools, we find dense packing of species and expected (or lower than expected) variance in SE Asia, tropical West and Central Africa, as well as along the highest terrestrial mountain ranges, the Andes and Himalayas, showing that high richness areas are prone to niche packing (Figure 4a). The Northern Hemisphere is characterised by expected assemblage evolutionary distinctiveness, with species filling expected or high volumes of morphospace, whilst having close neighbours present (Figure S10a,c). Under a phyloregional pool, the Central Highlands of New Guinea are one of few areas in tropical regions with lower morphological variance than expected (Figure 4b), with the western part of the range showing greater assemblage evolutionary distinctiveness than expected, highlighting it as an area with older lineages that are filling similar niches (Figure S10b,d). Oceanic islands tend to hold assemblages with species clustered in smaller volumes of trait space than expected, with many (i.e Galapagos etc.) also containing species representing greater than expected evolutionary distinctiveness (Figure S10b,d).

Environmental and evolutionary drivers of morphological diversity

Morphological variance$_{SES}$ (MV_{SES}) is associated with species richness, assemblage evolutionary distinctiveness$_{SES}$ and altitudinal range, but not with gross primary productivity (GPP), habitat heterogeneity and habitat type (Table S2). Global-pool MV_{SES} increases strongly before plateauing and subsequently declining with increasing species richness ($p < 0.001$: Figure 5a; Table S3), suggesting a pattern of morphospace expansion followed by packing at high species richness. MV_{SES} increases

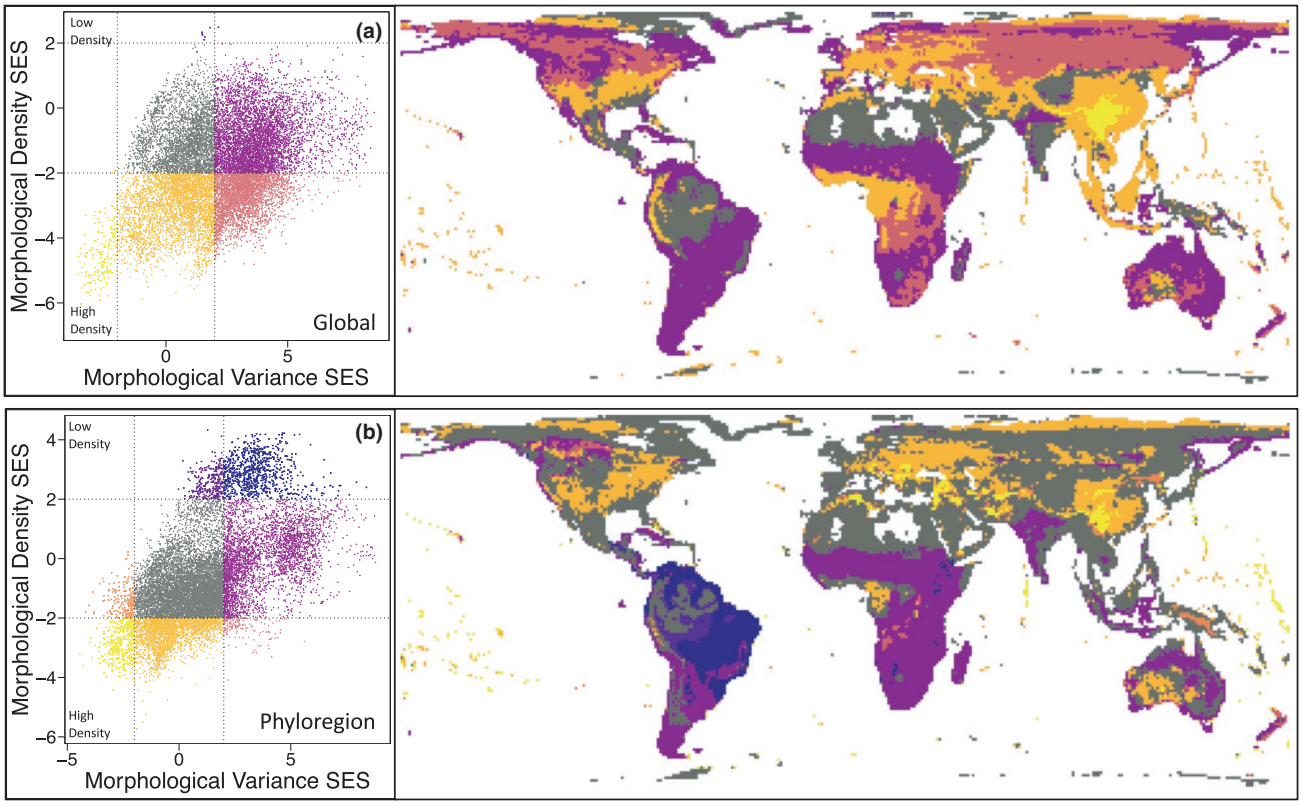

FIGURE 4 Areas of the globe where the standard effect sizes (SES) of different biodiversity metrics (morphological variance [sum of variances] and morphological density [mean nearest neighbour distance]) show statistically significant deviation from expected (+/− 2) for 8352 bird species across 15,980 terrestrial 1 degree grid cells under Behrmann projection. Combinations of variables are (a) morphological variance$_{SES}$ and morphological density$_{SES}$ where SES was calculated using global species pools, and (b) using phyloregional species pools. The grey colour shows no significant deviation from expected.

linearly with increasing evolutionary distinctiveness$_{SES}$ with the linear term ($p < 0.001$) and not the quadratic term ($p > 0.05$) significant (Figure 5b; Table S3). MV$_{SES}$ initially increases with altitudinal range from low (e.g. lowland plains, upland plateaus) to mid-elevational ranges before decreasing to lower levels where elevational range is greatest (e.g. montane slopes) ($p < 0.001$: Figure 5e; Table S3). We find no association between MV$_{SES}$ and GPP, and an almost flat relationship with habitat heterogeneity for just one subsample of our data (dataset D) ($p < 0.01$ (linear term only): Figure 5d; Table S3). Overall, we find broadly similar results when calculating phyloregional-pool MV$_{SES}$ (Figure 5f–j; Table S3).

Morphological density$_{SES}$ (MD$_{SES}$) is also associated with species richness, assemblage evolutionary distinctiveness$_{SES}$, altitudinal range and GPP, but not habitat heterogeneity or habitat type (Table S2). We find an initially flat relationship between global-pool MD$_{SES}$ and species richness, before distances between species sharply decrease as species richness increases ($p < 0.001$: Figure 5k; Table S3). Overall, we find a positive relationship between MD$_{SES}$ and assemblage evolutionary distinctiveness$_{SES}$, with species most spread out in trait space where assemblages have the highest assemblage evolutionary distinctiveness given species richness ($p < 0.05$: Figure 5l; Table S3). Species pack more closely in trait space than expected as energy availability (GPP) increases ($p < 0.05$: Figure 5m; Table S3). Assemblages are most packed at flat (e.g lowland plains, upland plateaus) and steep (mid-montane slopes) elevational ranges, with species most spread out at mid-elevational ranges ($p < 0.01$: Figure 5o; Table S3). No relationship between MD$_{SES}$ and habitat heterogeneity was found (Table S3). Under phyloregional pools, we find a contrast in model outputs where species richness is the predictor variable. As species richness increases, species become slightly less clustered in trait space than expected when using datasets B and D ($p < 0.01$ [linear term only]), but for dataset A, we find that species are most clustered in trait space (low MD$_{SES}$) at mid species richness values ($p < 0.05$) (Figure 5p; Table S3).

DISCUSSION

We present the first global mapping of a comprehensive set of continuous morphological traits, including three-dimensional bill shape data, for 8353 bird species, revealing regions of the world with exceptional relative spread and density of species traits. Our results suggest large-scale geographic variation in the relative importance of niche expansion and niche packing. Density

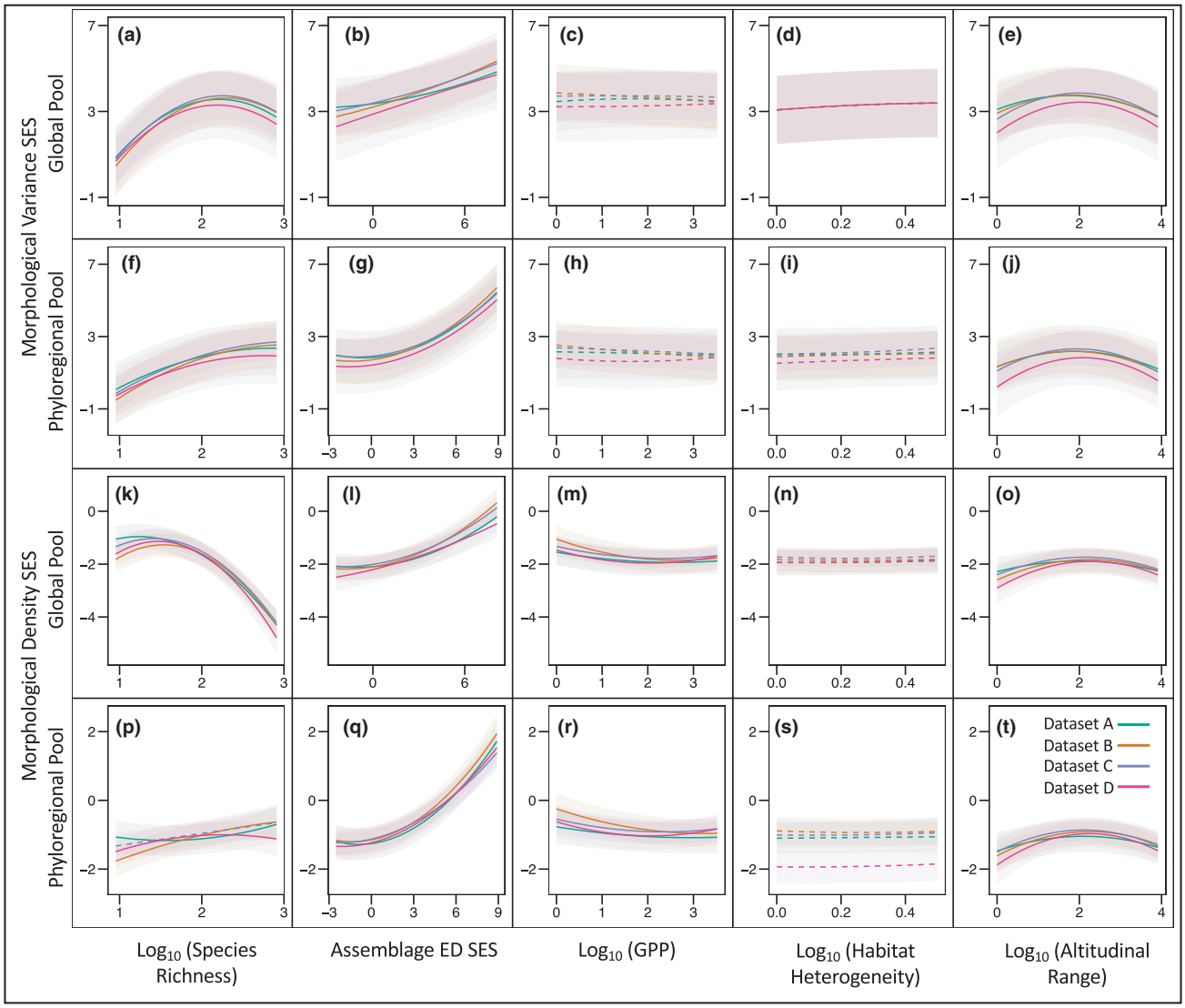

FIGURE 5 The effect of species richness, assemblage evolutionary distinctiveness (sum of equal splits) SES, gross primary productivity (GPP), habitat heterogeneity (Shannon's index), and altitudinal range on morphological variance (sum of variances) SES [generated from global (a-e) and phyloregional species pools (f-j)], and on morphological density (mean nearest neighbour distance) SES (generated from global (k-o) and phyloregional species pools (p-t)). High values of morphological density represent high mean nearest neighbour distances and therefore low density. Low values of morphological density represent low mean nearest neighbour distances and so high density. All raw variables (i.e. non-SES) are on a $\log_{10}$ scale. The lines represent predicted relationships from the multiple predictor gls models, with solid lines representing significant predictors whereas dotted lines are non-significant. Colours correspond to each 25% data subset (Dataset A = green, B = orange, C = purple, and D = pink).

and variance of morphological trait distributions scale with species richness and evolutionary distinctiveness, whereas only density scales with productivity (albeit weakly). Taken together, we suggest that evolutionary history plays a key role in shaping assemblage composition, particularly through niche expansion, whereas contemporary environment contributes more to niche packing.

Our use of global and phyloregional pools reveals the broad role of evolutionary history in shaping global assemblage structure. Tropical biodiversity hotspots, including the highland tropical Andes (Jarzyna et al., 2021), much of the central African tropics, and Indo-Malayan archipelago are densely packed compared to the global pool but not when compared to phyloregional faunas. In the same regions, variance follows global expectations but is higher than expected under the phyloregional null model. Such patterns would be expected if these hyper-diverse regions are both 'museums' where old species persist, and 'cradles' of diversity, where speciation rates are high (Gaston & Blackburn, 1996; Jablonski et al., 2006; McKenna & Farrell, 2006; Rolland et al., 2014). For instance, if morphological divergence is closely related to species age, surviving lineages will lead to greater morphospace volumes, and in addition, high numbers of closely-related young species will cause the denser packing of niche space in the tropics. In contrast, oceanic islands retain high density irrespective of the

species pool. Collectively these patterns imply a lasting imprint of distinct evolutionary and biogeographic histories on assemblage structure.

Areas of the Northern temperate regions tend to be more densely packed than expected, mirroring findings from smaller areas in the temperate lowlands using mostly categorical traits (Jarzyna et al., 2021). We also find a tendency for temperate assemblages to have higher morphological variance than expected under a global pool null model. Although it is difficult to directly infer the ecological drivers of community assembly using cell assemblage-based methods alone (Blanchet et al., 2020), our results hint that habitat filtering may contribute more to temperate, especially Northern Hemisphere regions, in shaping assemblage structuring. The observed pattern can only arise if morphospace is occupied by clusters of morphologically similar species, but where these clusters are spaced apart from one another. This would lead to high density within clusters, and high variance (the clusters are spread out across morphospace). This observation fits previous findings that standardised mean distance to centroid (functional dispersion) is greatest for birds in temperate and polar biomes (Cooke et al., 2019). Communities in the temperate and polar regions contain many species that migrate south during the Northern winter, with the remaining species likely to possess combinations of traits that allow survival over the harsh winter months (e.g. ecological guilds such as granivores and scavengers: Carnicer & Díaz-Delgado, 2008) leading to increased niche packing in these areas of morphospace.

The importance of evolutionary history for assemblage structure is further supported by our analyses of predictors of morphological diversity. Morphological diversity is expected to correlate strongly with species richness (Safi et al., 2011), as adding species must increase either volume or density. However, even after controlling for species richness using null models, we still find that species richness is a strong predictor of both morphological density and volume. Compared to both global and phyloregional models, morphological volume increases with species richness, suggesting niche expansion, before plateauing at high levels of species richness. This leads to increasing functional redundancy in species-rich regions (Oliveira et al., 2016). In contrast, and only for global models, niche space is exceptionally densely packed in areas of high species richness. This implies that niche packing becomes dominant in hyper-diverse assemblages, and mirrors findings that the similarity of bird species functional roles is highest in species-rich areas (Cooke et al., 2019).

Alongside species richness effects, we also find that assemblages with greater than expected evolutionary distinctiveness have both high variance and lower density in morphological space. This is consistent with the expected link between phylogenetic diversity and morphological diversity (Faith, 1992; Mazel et al., 2018; Safi et al., 2011) and suggests that niche expansion reflects phylogenetic history and the presence of more evolutionarily distinct species in hyper-diverse assemblages. In contrast, the combined increase in density with richness but decline with evolutionary distinctiveness implies that the packing of species in hyper-diverse assemblages is not a reflection of time since divergence. Instead, density, but not volume, increases with productivity. We suggest that assemblage morphospace expansion is driven by the accumulation of evolutionarily old lineages whereas packing is potentially the result of stable and productive environments supporting morphologically similar and evolutionarily young species. However, we note that the effects of productivity on morphological diversity are comparatively weak and therefore this interpretation ought to be treated with caution.

In addition to evolutionary history and productivity, we find some support for the expectation that heterogeneous habitats contain more niches, and can support morphologically more similar species, than homogenous ones (Kerr et al., 2001; Rahbek & Graves, 2001). As altitudinal range increases, morphological density decreases and volume increases, as species fill more niches resulting in a peak at mid-altitudinal ranges. The subsequent decline of morphological volume and increasing morphological density as species cluster in trait space at high altitudinal ranges (i.e. mid-montane slopes), is likely attributable to the high richness (α-diversity) (e.g. Davies et al., 2007) and turnover (β-diversity) (Graham et al., 2009) of closely related species (Voskamp et al., 2017), characteristic of such areas.

In our study, trait data were not available for all species, and biases in sampling could exist both phylogenetically and spatially (Figures S1 and S3) (Etard et al., 2020). For instance, certain groups, particularly those with rictal bristles or feathers obscuring the bill (e.g. nightjars and allies [Caprimulgiformes]), are under-represented because we were not able to obtain complete 3D bill scans. Globally, assemblages contain an average of 94% of species, with no assemblage containing less than 70% of species. Spatially, high richness areas are more likely to contain the greatest numbers of species with missing trait data, although these tend to be species from represented families with similar morphologies. We suggest, based on the phylogenetic (Figure S1) and spatial (Figure S3) structure of the missing data, that our analyses are unlikely to be strongly biased by missing data. We also suggest that the most likely impact of missing data is an underestimation of niche packing in high richness areas and a weaker relationship with productivity, although this is untested.

In conclusion, our work reveals novel insights into the structure and drivers of avian assemblages. We argue that evolutionary history plays a key role in shaping assemblage structure notably with evolutionarily old species contributing to niche expansion, and evolutionarily young species contributing to niche packing in the

tropics. We further suggest that tropical niche packing is facilitated by high productivity and potentially, though not directly tested here, the long-term stability of the tropics.

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AUTHORSHIP

E.C.H., D.P.E. and G.H.T. conceived the ideas and designed the methodology; E.C.H., J.A.B., E.J.R.C., C.R.C., G.H.T. and Z.K.V. collected data from museum specimens and designed analytical protocols for producing the beak shape dataset; E.C.H. analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13905.

DATA AVAILABILITY STATEMENT

The data and code supporting the results are available in the University of Sheffield's ORDA repository, provided by figshare: https://doi.org/10.15131/shef.data.16733224

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SUPPORTING INFORMATION

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RESEARCH ARTICLE

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The effects of tropical secondary forest regeneration on avian phylogenetic diversity

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Abstract

1. The conversion of tropical forests to farmland is a key driver of the current extinction crisis. With the present rate of deforestation unlikely to subside, secondary forests that regenerate on abandoned agricultural land may provide an option for safeguarding biodiversity. While species richness (SR) may recover as secondary forests get older, the extent to which phylogenetic diversity (PD)—the total amount of evolutionary history present in a community—is conserved is less clear. Maximizing PD has been argued to be important to conserve both evolutionary heritage and ecosystem function.
2. Here, we investigate the effects of secondary forest regeneration on PD in birds. The regeneration of secondary forests could lead to a community of closely related species, despite maintaining comparable SR to primary forests, and thus have diminished biodiversity value with reduced evolutionary heritage.
3. We use a meta-dataset of paired primary and secondary forest sites to show that, over time, forest specialist species returned across all sites as secondary forest age increased. Forest specialists colonize secondary tropical forests in both the Old World and the New World, but recovery of PD and community composition with time is only evident in the Old World.
4. *Synthesis and applications*. While preserving primary tropical forests remains a core conservation goal, our results emphasize the important role of secondary forest in maintaining tropical forest biodiversity. Biodiversity recovery differs between Old and New World secondary forests and with proximity to primary forest, highlighting the need to consider local or regional differences in landscape composition and species characteristics, especially resilience to forest degradation and dispersal capability. While farmland abandonment is increasing across marginal areas in the tropics, there remains a critical need to provide long-term management and protection from reconversion to maximize conservation benefits of secondary forests. Our study suggests such investments should be focused on land in close proximity to primary forests.

KEYWORDS

avian biodiversity, community composition, land-use change, secondary forest regrowth, tropical forest

1 | INTRODUCTION

The biggest driver of the current extinction crisis is the conversion of tropical forest to farmland (Laurance, Sayer, & Cassman, 2014). Over 150 million hectares of tropical forest were converted to farmland between 1980 and 2012 (Gibbs et al., 2010; Hansen et al., 2013). However, in many areas, agricultural land has been abandoned resulting in the regeneration of secondary forests (Aide et al., 2013). These secondary forests could help to reduce biodiversity loss (Chazdon, 2014) by providing an alternative to primary forests for species that would otherwise go extinct (Wright & Muller-Landau, 2006). Species richness (SR) often recovers with secondary forest age (Acevedo-Charry & Aide, 2019; Barlow, Mestre, Gardner, & Peres, 2007; Gilroy et al., 2014), and many forest specialists that are threatened by forest loss may also recolonize secondary forests (Basham et al., 2016; Gilroy et al., 2014). However, our understanding of how biodiversity metrics other than SR differ between primary and secondary forests is limited.

One such gap in our knowledge is whether secondary forests conserve or support recovery of phylogenetic diversity (PD)—the total amount of evolutionary history present in a community (Faith, 1992). PD is potentially important for several reasons. First, while functional diversity—the range of functional roles occupied by species within a community (Petchey & Gaston, 2006)—and PD may not be perfectly correlated, prioritizing the conservation of PD is also expected to conserve functional diversity (Faith, 1992; Mazel, Mooers, Riva, & Pennell, 2017; Mazel et al., 2018; Pavoine, Gasc, Bonsall, & Mason, 2013). Functional redundancy increases as secondary forest age increases, potentially leading to greater resilience in ecosystem services (Sayer, Bullock, & Martin, 2017). Moreover, it has been argued that conservation objectives focused on a narrow set of functional traits could lead to the loss of PD. This is because there are many potential axes of functional diversity that are typically condensed to a subset of traits that are easy to measure and/or widely available. Instead, PD may more effectively capture a wide suite of traits encapsulated under the concept of feature diversity, defined broadly as the different evolutionary features of diversity (Faith, 1992; Owen, Gumbs, Gray, & Faith, 2019). Second, phylogenetically diverse communities are more likely to hold evolutionarily distinct or relict species with few close relatives (Jetz et al., 2014) and so harbour a disproportionately large amount of evolutionary history. Third, there is intrinsic value in conserving as much of the world's evolutionary heritage as possible (Winter, Devictor, & Schweiger, 2013). Therefore, understanding how PD recovers and the mechanisms that drive this recovery is critical to understanding the conservation potential of secondary tropical forests.

Recovery of SR alone is unlikely to be an informative guide to the conservation value of secondary forests as SR (i.e. alpha diversity) tells us nothing about community composition. Conversion of forest to agriculture could result in the loss of forest-dependent or disturbance-sensitive species, and the gain of disturbance-tolerant species or species adapted to more open habitats. As such, whilst SR may recover rapidly following abandonment, it may markedly differ in community structure, phylogenetic composition, and ecosystem function. However, subsequent succession towards secondary forest may allow the return of forest-dependent species. Large frugivores and understorey insectivores, for example, are particularly forest dependent and sensitive to disturbance (Powell et al., 2015; Şekercioğlu, 2012; Şekercioğlu et al., 2002) so may require time for secondary forest to mature before returning. In addition, species with low dispersal abilities may have a reduced ability to recolonize secondary forests (Laurance & Gomez, 2005; Moore, Robinson, Lovette, & Robinson, 2008), particularly if secondary forest patches are far from the remaining primary forest source pool.

At one extreme, the same set of species originally found in the primary forest prior to conversion to agriculture could recolonize the secondary forest resulting in the simultaneous recovery of SR, community composition, and PD. At the other extreme, community intactness may be substantially degraded. PD in intact primary forest tends to be greater than expected by chance and rapid land-use change results in phylogenetic clustering of communities as PD is lost rapidly with increasing agricultural intensification (Frishkoff et al., 2014; Prescott et al., 2016). This leads to the prediction that young secondary forests should have low PD compared to primary forests whereas differences in SR may be comparatively minor. If secondary forest provides a viable alternative habitat for primary forest species, then PD should increase with age as the forest matures (e.g. Edwards, Massam, Haugaasen, & Gilroy, 2017). The effect of variability in species traits and of the landscape matrix is that recovery of SR, community composition and PD may be further mediated by the degree of isolation of secondary forest patches, with stalled or slow recovery in the most isolated secondary forests.

Here, we conduct the first pan-tropical assessment of change in PD with secondary forest age. We focus on birds, because they are functionally important components of ecosystems (Şekercioğlu, Wenny, & Whelan, 2016). Specifically, we assess if SR and PD vary between primary and secondary forests and whether the secondary forest communities attain comparable SR and PD to paired primary forest communities as time since abandonment increases. We further assess how distance to primary forest, biogeography (Old World vs. New World) and climate mediate variation in the recovery of tropical forest bird communities.

2 | MATERIALS AND METHODS

2.1 | Data collation

A total of 20 pan-tropical studies containing 35 paired secondary and primary forest sites were selected from a review by Sayer et al. (2017; see Data Sources and Table S1). Seven sites included by Sayer et al. (2017) were considered unsuitable for the present study (i.e. due to incomplete species lists, ambiguous secondary forest ages, etc.) and were excluded (Appendix S1). All sites included were in the tropics and subtropics with 21 in the New World and 14 in the Old World (Figure 1). Primary forest sites are native forests with no evidence of previous deforestation and degradation. Secondary forest sites are defined as areas undergoing succession after all or nearly all trees had been removed to make way for agriculture (Corlett, 1994). Forests recovering after fires

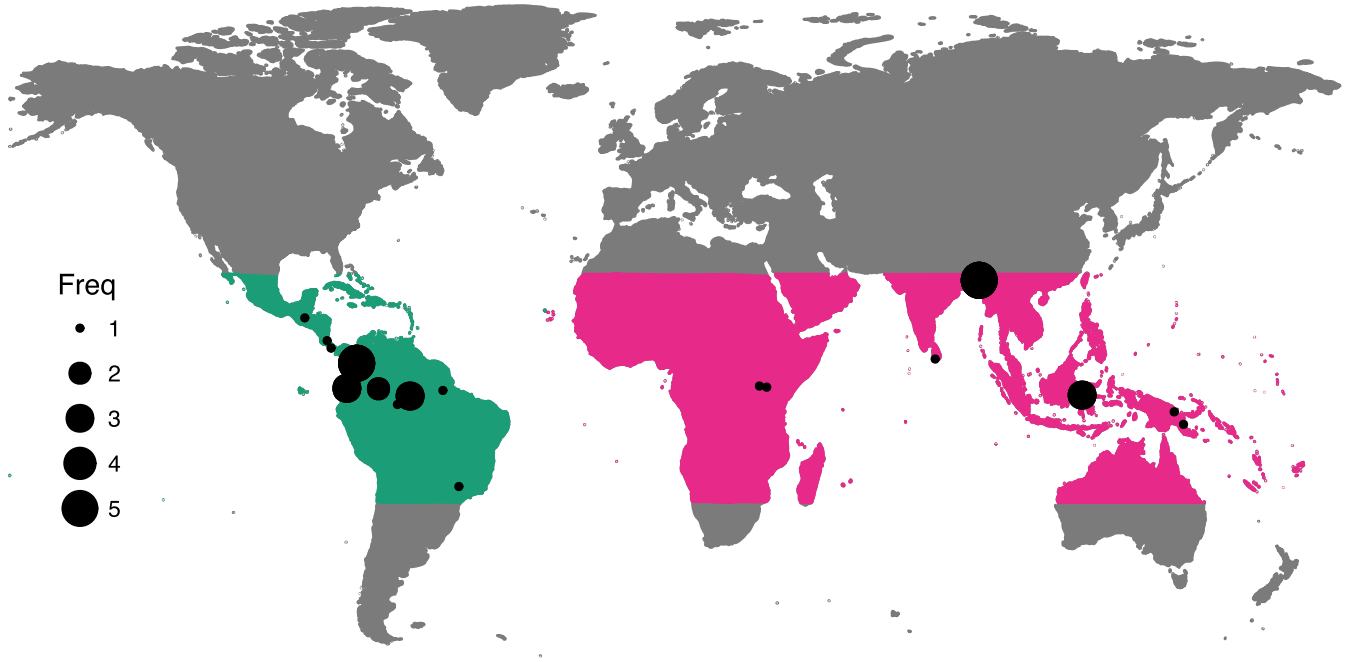

FIGURE 1 The distribution of the 35 paired sites in this study. Sites were chosen within 24 degrees of latitude from the equator. The number of paired sites per study area is indicated by circle size. The New World is coloured green and the Old World is coloured pink

or sites that had been selectively logged were not included in this definition.

The ages of secondary forest sites were given in each study as single ages or age ranges where similarly aged stands were grouped together. In the latter instance, the median values of secondary forest patches were calculated (Sayer et al., 2017). Where available, we extracted the distances between paired primary and secondary forest sites from measured values, or qualitative descriptions given in the studies considered (n = 31; Table S1). Each of the chosen studies sampled the entire local avian community in both primary and secondary forest patches using consistent methods within studies, but which varied between studies (i.e. point counts, mist netting, transects). Specific information regarding how each species observed used the habitat (e.g. foraging, breeding, etc.) were not described.

We also collected data for three environmental variables at each site. Elevation (metres above sea level) for each site was obtained from the GTOP030 global digital elevation model (GTOPO30 DEM, 1996) using Google Earth Engine (Gorelick et al., 2017). Mean annual temperature and mean annual precipitation were extracted for each site from the WorldClim database (Fick & Hijmans, 2017). Elevation, precipitation and temperature were log-transformed prior to analysis.

2.2 | Measures of species richness and phylogenetic diversity

For each study site, we calculated the number of different species present in each community (SR), and beta diversity (*ßTD*; Whittaker, 1960, 1972), and phylogenetic beta diversity (*ßPD*; Bryant et al., 2008; Graham & Fine, 2008) as measures of community intactness, for each paired primary and secondary forest site. We calculated the Sørenson index in the R package VEGAN (version 1.4-2: Oksanen et al., 2008) as a measure of *ßTD*, to assess the losses of species from each secondary forest site compared to the corresponding paired primary site. *ßPD* was measured as a fraction of the phylogenetic branch lengths present in secondary forest communities that were also present in paired primary forest communities using the *phylosor* function in the R package PICANTE (version 1.6-2: Kembel et al., 2010).

We also calculated three PD metrics and their standardized effect sizes using the R package PICANTE (version 1.6-2: Kembel et al., 2010). These were: phylogenetic diversity (PD, the total amount of evolutionary history represented by a community; Faith, 1992); mean pairwise difference (MPD, average phylogenetic distance between every combination of paired individuals in a community; Webb, Ackerly, McPeek, & Donoghue, 2002); and the mean nearest taxon distance (MNTD, average phylogenetic distance between an individual and its closest relative in the community; Webb et al., 2002). Because PD, MPD and MNTD can all scale with SR (Webb et al., 2002) we calculated standardized effect sizes for each raw PD measure using the 'richness' algorithm in PICANTE. This maintains SR for each site but allows the random selection of species from a wider species pool (Webb et al., 2002). We refer to these metrics as ses.PD, ses.MPD and ses.MNTD respectively. A full description of the metrics, including the equations used, is available in the Table S2.

Species pools were generated by downloading species lists from http://mol.org/ (Map of Life, 2017) for a 50-km radius around each study site. Map of Life uses species range maps (e.g. BirdLife International), as well as data from additional sources such as point count data from published studies. A 50-km radius was chosen for three reasons. Firstly, it allows the inclusion of all species that are likely to occur at each site. Secondly, previous studies have shown

that finer spatial resolutions are not practical given the quality of range maps, and can give an inaccurate representation of observed species pools (Hurlbert & Jetz, 2007). Thirdly, the Map of Life database only allows for a radius of 50 km to be selected. Including all species within a 50-km radius of each site could result in species appearing that would never occur at our sites, particularly in areas that are topographically diverse or at the margins of distinct biomes. To investigate the impact of changing species pools, we ran analyses on subsets of our species pools (all species, and forest only species), and found similar results in both instances (Tables S5 and S6).

We downloaded 500 phylogenetic trees based on the Hackett backbone (Hackett et al., 2008) from http://birdtree.org/ (Jetz, Thomas, Joy, Hartmann, & Mooers, 2012) and calculated all metrics on every tree to account for phylogenetic uncertainty. For each measure of PD and for *ßPD*, the 500 values were found to be normally distributed and an arithmetic mean value was taken for each site or paired site community.

2.3 | Statistical analysis

We used linear mixed-effects models in the LME4 R package (version 1.1-13: Bates, Mächler, Bolker, & Walker, 2014) with RStudio version 1.0.136 (RStudio Team, 2016) and R version 3.3.2 (R Core Team, 2016). We included study identity as a random effect in all models because study areas included multiple secondary forest sites with a single primary forest site (Table S1). As differing evolutionary histories and biogeographic variation in dispersal may influence PD recovery patterns, we compared New World and Old World sites. For each analysis, models were constructed with either the fixed effect of forest type (primary or secondary), or secondary forest age and distance between primary and secondary sites, as well as the random effect of study identity. Secondary forest age and distance between primary and secondary sites were log-transformed. These models were compared to a null intercept only model, with study identity as a random intercept. Residuals for each model were checked for normality and homoscedasticity. Likelihood ratio tests (LRTs) were used to compare models. We added our three climatic predictors in turn to the best-fitting age and distance models for each response variable and region combination.

2.3.1 | Primary versus secondary forests

We analysed the effect of forest type on SR and each of the raw PD metrics.

2.3.2 | Species and phylogenetic community composition

We tested the effect of secondary forest age, and distance between paired primary and secondary forest sites, on community intactness. We calculated community intactness for *ßTD* and *ßPD* between paired primary and secondary forest sites using a restricted species pool containing just primary forest species (n = 1,179).

2.3.3 | Species and phylogenetic diversity

We next examined changes in PD with time since secondary forest abandonment. We calculated our metrics on all species (n = 1,519), and also on a reduced subset, excluding species that were defined by BirdLife International as 'Non-forest' (does not normally occur in forested habitat). The remaining 1,478 species were categorized as having either 'High' (forest specialists, always or nearly always recorded in primary forest), 'Medium' (largely found in primary forest, but often occurs and can breed, in degraded habitat) or 'Low' (can occur in primary forest, but more often found and breeds, in degraded habitat) forest dependency (Birdlife International, 2017; Buchanan et al., 2008; Figure S1). When considering only forest species in our analyses, we likewise reduced the species pools used for calculating standardized effect sizes by removing species that were defined as not dependent on forests (Birdlife International, 2017).

We calculated the log response ratio (Hedges, Gurevitch, & Curtis, 1999) as the log proportional difference between the means of each metric (SR, PD, MPD, MNTD) in secondary forest sites and primary forest sites. Values of ses.PD, ses.MPD and ses.MNTD can be negative, and so raw differences between paired secondary and primary forest were calculated.

2.3.4 | Forest-dependent species

We investigated whether the proportion of forest-dependent species at each site became more equal as secondary forest age increased. For each site, we calculated the percentage of the avian community that were classed by Birdlife International (2017) as having 'High' forest dependency, before calculating the difference between those percentages for each paired secondary and primary forest sites.

3 | RESULTS

Across all study sites, 1,519 unique species were recorded spanning 87 avian clades (Figure 2). We found large clades in Old World sites with similar numbers of species found in both primary and secondary forest types (i.e. Shrikes and Monarchs, Pigeons and Doves, Cuckoos), with the exception of the Chats and Old World Flycatchers with higher SR in secondary forest sites. Some families with only a single species represented across all study sites were present in primary but not secondary forests (e.g. Whipbirds and Allies: *Ptilorrhoa caerulescens*, Bowerbirds: *Ailuroedus buccoides*).

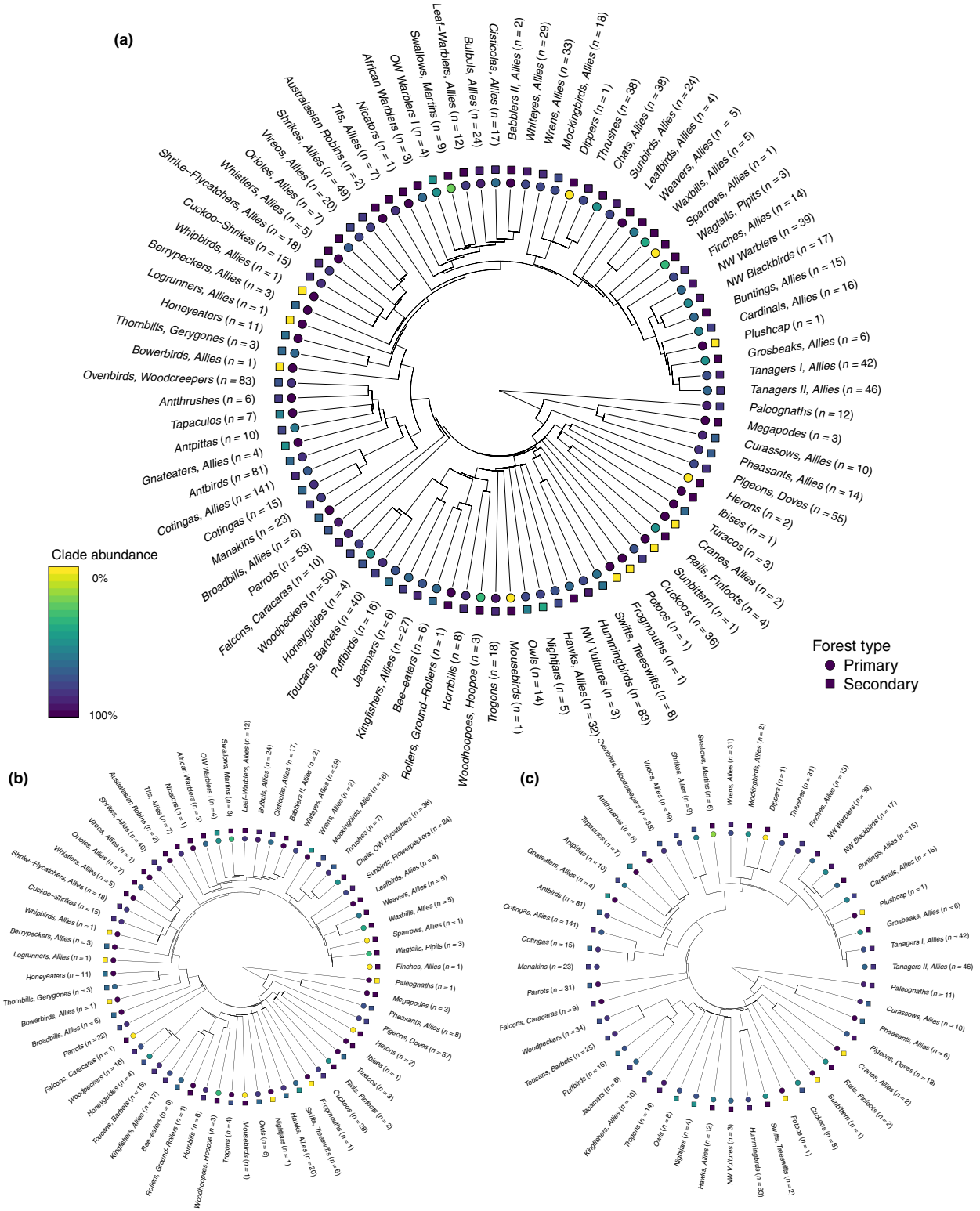

FIGURE 2 Phylogenetic distribution of avian clades in secondary and primary forests across (a) all study sites, (b) Old World sites and (c) New World sites. Spots and squares show a clade's presence in primary and secondary forest respectively. The colour scale bar shows the proportion of species in a clade which is found in that particular habitat type

In the New World, many avian clades were species rich in both primary and secondary forests (e.g. Woodpeckers, Trogons, Manakins and Cotingas; Figure 2c). Some very small clades were present in only primary (Potoos and Sunbittern) or only secondary forest sites (e.g. Sparrows and Dippers). Several young passerine clades (e.g. Tanagers, Grosbeaks, Cardinals, Buntings, New World Blackbirds, New World Warblers) were more species rich in secondary than primary forests.

3.1 | Primary versus secondary forests

Primary forests had a similar SR to secondary forests across the tropics (LRT: $\chi^2 = 1.01$, $p = 0.315$), in the New World (LRT: $\chi^2 = 0.26$, $p = 0.609$), and in the Old World (LRT: $\chi^2 = 1.43$, $p = 0.232$). PD did not differ between primary forests and secondary forests across all sites (LRT: $\chi^2 = 2.45$, $p = 0.118$), Old World sites (LRT: $\chi^2 = 2.63$, $p = 0.105$) or New World sites (LRT: $\chi^2 = 0.52$, $p = 0.469$). Similarly, we found no differences in ses.PD, MPD, ses.MPD, MNTD or ses.MNTD between primary and secondary forests, in the New World, Old World and across all sites (Table S3).

3.2 | Species and phylogenetic community composition

Avian communities in paired secondary and primary forest sites in the Old World became increasingly similar in both species (*ßTD*; Figure 3a; Table S4; LRT: $\chi^2 = 17.71$, $p < 0.001$) and phylogenetic (*ßPD*; Figure 3b; Table S4; LRT: $\chi^2 = 19.51$, $p < 0.001$) composition with increasing time since abandonment. Based on estimated slopes, secondary forest species and phylogenetic composition would equal that of primary forests after 97 and 92 years respectively. In the Old World, distance between secondary and primary forest sites did not influence phylogenetic (LRT: $\chi^2 = 0.16$, $p = 0.685$) or species community intactness (LRT: $\chi^2 = 0.19$, $p = 0.665$; Figure 3c,d; Table S4). We also found a significant interaction with distance for both *ßTD* and *ßPD* where recovery appeared to be more rapid in more isolated sites (Table S4). We suggest that the counterintuitive result may be spurious because only three Old World sites are isolated from primary forest, and in those sites, distance and age have a perfect rank correlation.

We found no change in *ßTD* (LRT: $\chi^2 = 0.01$, $p = 0.923$) or *ßPD* (LRT: $\chi^2 = 0.05$, $p = 0.827$) between paired primary and secondary forest communities in the New World as time since disturbance increases (Figure 3a,b; Table S4). Indeed, soon after land abandonment, New World communities retained around 72% of species and 79% of phylogenetic intactness compared to primary forest communities, and this did not significantly change across the 50-year study period. However, we found that as distance between sites increases, the number of primary forest species that are found in New World secondary forest sites decreases (LRT: $\chi^2 = 5.43$, $p = 0.020$), but that phylogenetic intactness (LRT: $\chi^2 = 3.30$, $p = 0.069$) did not change (Figure 3c,d; Table S4). We found no effect of any of the climatic predictors on species or phylogenetic community intactness (Table S8).

3.3 | Species and phylogenetic diversity

Across all sites, relative SR did not increase with secondary forest age (LRT: $\chi^2 = 2.22$, $p = 0.137$). However, in the Old World, as secondary forest age increased relative SR recovered (LRT: $\chi^2 = 6.39$, $p = 0.011$) and reached primary forest levels in ~46 years (Figure 4a; Table S5). As with our analysis of community intactness above, we found a significant but weak interaction between age and distance. Secondary forest age did not have a significant effect on SR in the New World (LRT: $\chi^2 = 0.01$, $p = 0.928$). We found a positive effect of secondary forest age on PD recovery in the Old World (LRT: $\chi^2 = 4.01$, $p = 0.045$),

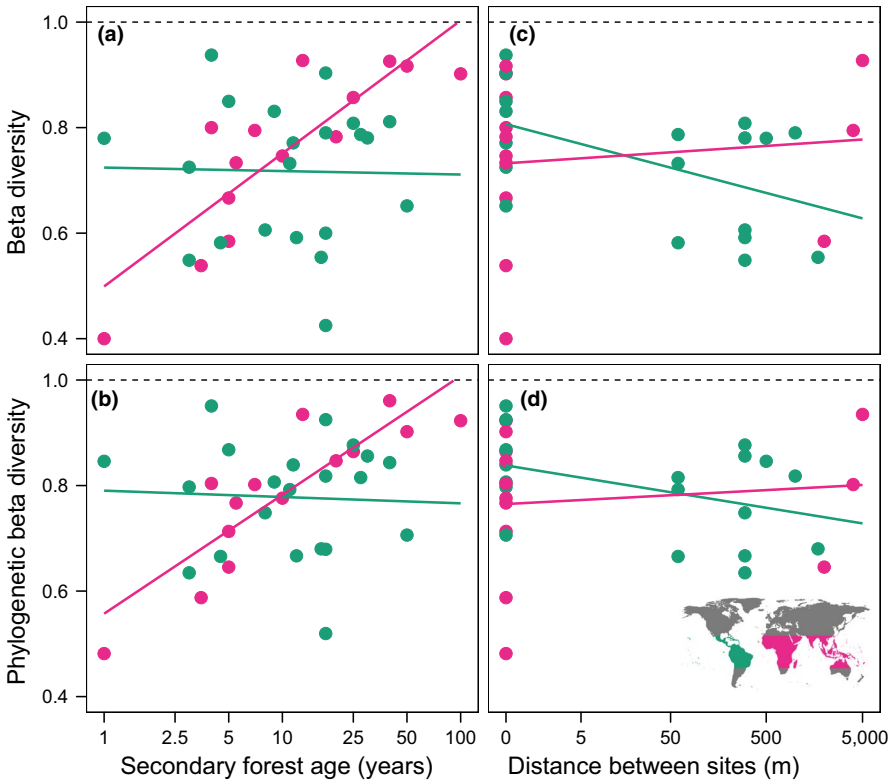

FIGURE 3 The effect of secondary forest age on (a) *ßTD* and (b) *ßPD* and the distance between primary and secondary forest sites on (c) *ßTD* and (d) *ßPD* in the New World (green) and Old World (pink). Secondary forest age is plotted on a log10 scale. On both *y*-axes, values fall between 0 (primary and secondary forests are dissimilar) and 1 (primary and secondary forests are similar). Lines of best fit were plotted from the fixed effects output of our mixed-effects models. The dotted line represents the value at which primary and secondary forests are identical

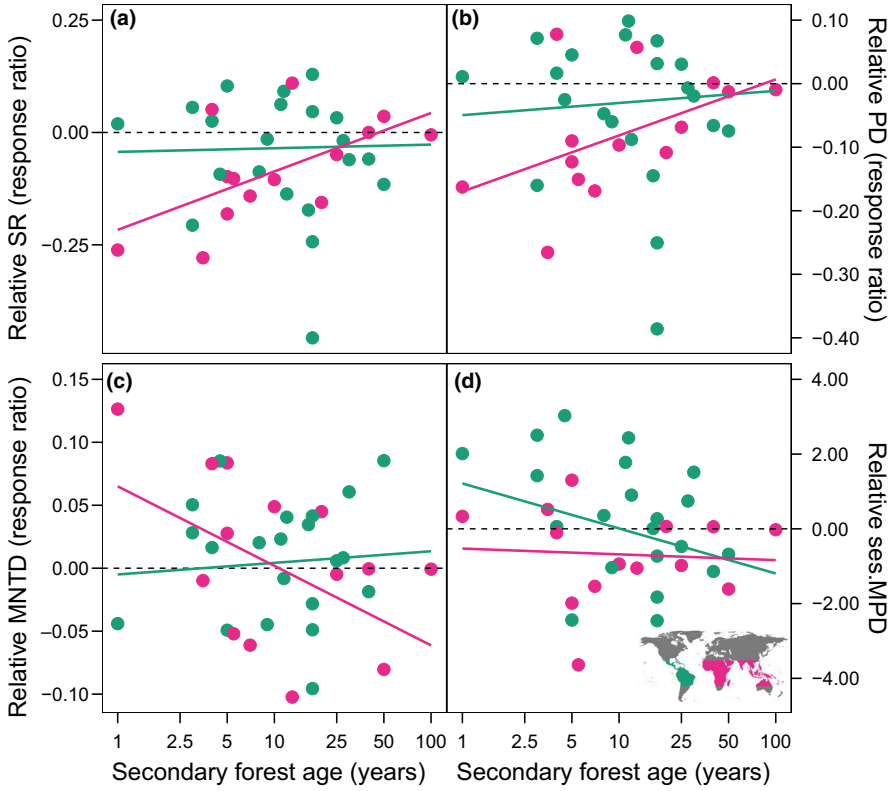

FIGURE 4 The effect of secondary forest age on (a) relative species richness (SR), (b) relative phylogenetic diversity (PD), (c) relative mean nearest taxon distance (MNTD) and (d) relative ses. MPD in the New World (green) and Old World (pink). Secondary forest age is plotted on a log10 scale. If SR, PD, MNTD or ses.MPD is lower in secondary forests compared to primary forests, values on the y-axis will be negative and vice versa. Lines of best fit were plotted from the fixed effects output of our mixed-effects models. The dotted line highlights where SR, PD, MNTD and ses.MPD are equal in both primary and secondary forests

with PD reaching primary forest levels ~84 years after disturbance (Figure 4b; Table S5). Secondary forest age did not have a significant effect on PD in the New World (LRT: $\chi^2 = 0.08$, $p = 0.782$). Secondary forest regeneration time had no effect on ses.PD levels in the New World, Old World or across all sites (Table S5).

Across New World sites, relative ses.MPD decreased as secondary forest age increased (LRT, $\chi^2 = 4.40$, $p = 0.040$; Figure 4c; Table S5). This indicates that species within communities become more closely related to each other as secondary forest age increases. We found no effect of secondary forest age on ses.MPD in the Old World or across all sites (Table S5). Relative MNTD decreased in the Old World as secondary forests get older (LRT, $\chi^2 = 4.31$, $p = 0.038$; Figure 4d; Table S5). No change in relative MNTD was found in the New World or across all sites (Table S5). Secondary forest age did not predict relative MPD, MNTD or ses.MNTD in the New World, Old World and across all sites, with models containing secondary forest age not significantly explaining the data better than null models. Adding climatic variables to our best-fitting age and distance models did not improve model fit for any metric of richness or PD (Table S8).

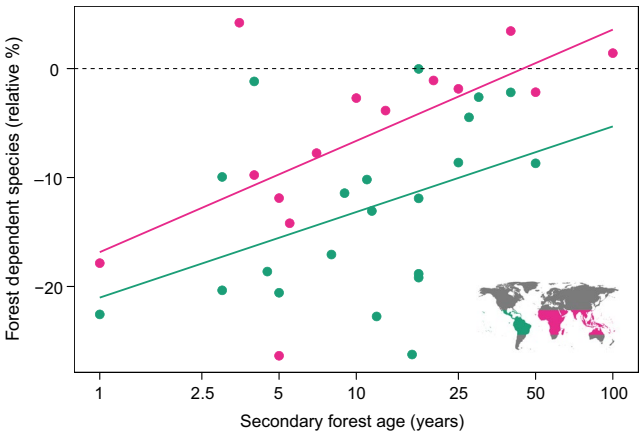

FIGURE 5 The effect of secondary forest age on the proportion of highly dependent forest species found in secondary forest communities when compared to the paired primary forest site in the New World (green) and Old World (pink). Secondary forest age is plotted on a log10 scale. Lines of best fit were plotted from the fixed effects output of our mixed-effects models. The dotted line highlights where the proportion of highly dependent forest species in a community is equal in both primary and secondary forests

3.4 | Forest-dependent species

We found that the relative proportion of forest-dependent species increased with secondary forest age across all sites (LRT: $\chi^2 = 9.55$, $p = 0.002$), New World (LRT: $\chi^2 = 4.12$, $p = 0.043$) and Old World sites (LRT: $\chi^2 = 7.02$, $p = 0.008$; Figure 5; Table S7). Indeed, there were an equal percentage of forest-dependent species in paired primary and secondary forest sites in the Old World after 45 years. However, after 50 years of secondary recovery in the New World, there were still 7.7% fewer forest-dependent species in secondary forests, compared to primary forests. The proportion of forest-dependent species declined with increasing temperature when temperature was added to the best-fitting age and distance model, but only for the New World and global analyses. No other climatic variables improved model fit (Table S8).

4 | DISCUSSION

Our study represents the first global assessment of recovery of avian PD in secondary tropical forests. Our results confirm that secondary forests can act as important reservoirs of PD, particularly in landscapes with little remaining natural forest (Frishkoff et al., 2014). Overall, we find that avian PD recovers towards primary forest levels as Old World secondary forests become older, reaching equivalence at around 100 years, but that this level of recovery is not evident in New World secondary forest. Importantly, this pattern is not driven by the colonization of a closely related set of species, but by the same set of species found in primary forests returning to Old World secondary forests sites over time (as highlighted by increasing community intactness with age). This suggests that, at least in the Old World, forest specialist species that are threatened by forest loss are returning to secondary forests. In New World secondary forests, previous work has shown that both SR (Dunn, 2004) and PD (Edwards et al., 2017) recover as secondary forest age increases. Our findings from the Old World support the hypothesis that secondary forest regeneration can lead to comparable biodiversity to those found in primary forests and that PD recovers concomitantly with SR as the set of species that colonize secondary forest during recovery is drawn from the primary forest pool.

Previous studies (e.g. Edwards et al., 2017; Frishkoff et al., 2014) found that the conversion of primary forest to agricultural land can initially lead to phylogenetic clustering, with the avian community containing species that are on average much more closely related to each other in evolutionary time. If secondary forest allows recovery of avian communities, then we might expect to see the trend reversed with increasing PD and decreasing clustering through time. Our results are partially consistent with this prediction, but suggest a more nuanced dynamic of gains of forest species alongside loss of non-forest, open habitat species. In both the Old and New World, the proportion of forest-dependent species increases with secondary forest age, although the effect appears to be weaker in the New World, at least with respect to our sampled sites. In the Old World, this is concomitant with increases in SR and PD. In the New World, neither SR nor PD increases with age.

The degree of phylogenetic clustering, however, appears to increase with age in both the Old World and the New World. This result is best explained by the gradual shift from open/agricultural habitats to mature forest, as opposed to the abrupt change associated with deforestation in the reverse direction. Avian communities in the early stages of recovery are likely to consist of resilient open habitat species (Acevedo-Charry & Aide, 2019), those from younger clades (Edwards et al., 2017; Frishkoff et al., 2014), species with wide diet breadths (e.g. granivores; Frishkoff et al., 2014) and the most resilient forest-dependent species. Over time, the gain of forest species seems to outweigh the loss of open habitat species, leading to net gains in SR and total PD (although this was only observed in the Old World in our data). However, the community becomes increasingly dominated by a more closely related set of forest specialists returning and becoming more common (e.g. understorey insectivores: Acevedo-Charry & Aide, 2019; Stratford & Stouffer, 2015). This turnover-driven pattern is borne-out by considering analyses using species pools including all species compared to species pools with only forest-dependent species: the clustering trends are much weaker or absent in analyses including only forest-dependent species. If this pattern of recovery continues steadily over time, then we would expect to observe trends that eventually lead to clustering patterns that are similar to those in primary forests. The absence of this pattern in our data suggests that secondary forest may take a longer period of time than that captured in our dataset for to mature. If so, then some of the most forest-dependent species may have not yet returned, and indeed may never return (Acevedo-Charry & Aide, 2019; Sayer et al., 2017). In both our Old and New World samples, species from some clades represented in primary forest do not appear in secondary forest sites and are also among the most phylogenetically distinct, such as Potoos and Sunbittern in the New World and the Nightjars and Frogmouths in the Old World.

While forest species appear to increasingly colonize secondary forest communities over time in both the Old and New World, community composition recovers with age in the Old World but not the New World where paired primary and secondary forests hold 72% of the same species, and this does not significantly change across the 50-year study period. This could be interpreted as evidence for hemispheric differences in the response of species and such differences could be the result of largely independent evolutionary histories. However, we suggest a more parsimonious explanation due to differences in the sites included in our meta-dataset. Specifically, in the Old World, the majority of paired sites are contiguous such that secondary forest abuts primary forest. Only three sites in our Old World data are not connected (and are also the most distant sites within the entire dataset). Effectively, and by chance, this controls for potential confounding effects of distance and the role of species-specific dispersal in determining patterns of recovery. In contrast, New World sites are rarely contiguous and distances between secondary and primary forest sites are highly variable (ranging from 0 to 1,725 m). Indeed, our models including distance between sites suggested lower recovery as distance increases. That is, in the New World recovery by distance may mask any effect of recovery by age. We are cautious in our interpretation because the distance data are incomplete and, in some cases, qualitative rather than quantitative.

An alternative explanation for our finding that PD recovery differs in the Old and New World could be a difference in species dispersal potential. Moore et al. (2008) found that some Neotropical species in Panama were unable to fly 100 m, and similarly, passerines from the families Formicariidae and Thamnophilidae in the Brazilian Amazon failed to cross 250 m over farmland to reach their territories (Laurance & Gomez, 2005). While bird groups with poor dispersal ability, such as the wren-babblers (Timallidae), do occur in the Old World, there may be disproportionately more poorly dispersing species in the New World. At present, detailed data on the dispersal ability of many tropical birds are lacking. Nonetheless, identifying whether New World species share any dispersal, or colonization, limiting traits could suggest that region- and ecology-specific conservation strategies are required for secondary forest management.

5 | CONCLUSIONS

5.1 | Management implications

The rate of deforestation of primary tropical forests is unlikely to slow. In some regions that have experienced high levels of primary forest loss in agriculturally suitable areas, the area of space occupied by secondary forests is increasing as farmland is abandoned. For instance, in Latin America and the Caribbean, >360,000 km^2 of new secondary growth occurred between 2001 and 2010 (Aide et al., 2013). Furthermore, each year around 290,000 km^2 of secondary forest regrowth occurs on abandoned land globally (Hurtt et al., 2017). Abandonment is most likely to happen in marginal areas that are too dry or steep for more modern farming methods (de Rezende, Uezu, Scarano, & Araujo, 2015; Sloan, Goosem, & Laurance, 2016), and it is these marginal areas that perhaps pose the biggest opportunities for conservation gains (Edwards et al., 2017; Gilroy et al., 2014).

Forest connectivity, the sizes of primary forest patches and human activity could influence the rate at which species can recolonize secondary forests following abandonment (Banks-Leite, Ewers, & Metzger, 2012; Maldonado-Coelho & Marini, 2000; Prugh, Hodges, Sinclair, & Brashares, 2008). The majority of secondary forests are reportedly found in close proximity to remnant forest across the tropics (Crk, Uriarte, Corsi, & Flynn, 2009; Edwards et al., 2017; Sloan et al., 2016), and it is therefore likely that primary forest patches acted as sources of colonizing dispersers to secondary forest patches across all sites in our study (Gilroy & Edwards, 2017). Indeed, in the Old World, the majority of secondary forest sites are contiguous with primary forest sites.

Although secondary forest regeneration is likely to occur in areas that are unsuitable for modern farming practices, they still face the threat of deforestation. Indeed, in Costa Rica, 50% of secondary forests were found to have been cleared within 20 years, and 84% within 54 years (Reid, Fagan, Lucas, Slaughter, & Zahawi, 2018). In both the Old and New World, using carbon-based payments for ecosystem services under REDD+ to protect these new forests from deforestation or to enhance the rate with which land is abandoned and returned to secondary forest (Gilroy et al., 2014) represents a key conservation opportunity. Furthermore, the emerging global Forest and Landscape Restoration agenda, in which nations have targeted 350 million hectares of restoration by 2030 (Bonn Challenge, n.d.; GPFLR, 2003), represents another policy driver for the recovery of secondary forests. Such investments should be focused on land in close proximity to primary forests, which our study suggests would enhance the rate of recovery of diversity. In addition, regenerating forests tend to be poorly protected, with laws, policies and socioeconomic conditions that can work against long-term persistence. In Costa Rica, for example, the laws that protect forests exclude young, regenerating sites; in fact, they are often targeted for clearing to prevent them being reclassified as forest (Sierra & Russman, 2006). We thus need to focus our attention on legal frameworks to remove disincentives to the longer term persistence of secondary forests.

Taken together, our results not only point to an important role of secondary forest in maintaining tropical forest biodiversity but also suggest the critical need to provide long-term management and protection to maximize conservation benefits. We also highlight the importance of integrating local and regional patterns of fragmentation and landscape ecology when investigating the potential of secondary forests to safeguard biodiversity (Arroyo-Rodríguez et al., 2017). Secondary forests are likely to be at constant threat of reconversion to farmland (Reid et al., 2018; Sánchez-Cuervo & Aide, 2013; Sodhi et al., 2010) and given that agricultural land has far lower SR and PD than does secondary forest (Edwards et al., 2017), protection of secondary forests should be seen as a priority for the conservation of tropical biodiversity.

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AUTHORS' CONTRIBUTIONS

E.C.H., D.P.E. and G.H.T. conceived the ideas and designed methodology; E.C.H., C.A.S. and P.A.M. collected the data; E.C.H. analysed the data; E.C.H. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

This paper brings together data from a number of published studies which are referenced in the Data Sources section below, and outlined in Table S1. C. Banks-Leite, D. Becker, S.H. Borges and B. Maas, provided access and permission to use additional data for this study. Our generated data are available via the Dryad Digital Repository https://doi.org/10.5061/dryad.0p2ngf1ww (Hughes, Edwards, Sayer, Martin, & Thomas, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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