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Diversity and extinction risk are inversely related at a global scale

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Abstract

Increases in biodiversity often lead to greater, and less variable, levels of ecosystem functioning. However, whether species are less likely to go extinct in more diverse ecosystems is unclear. We use comprehensive estimates of avian taxonomic, phylogenetic and functional diversity to characterise the global relationship between multiple dimensions of diversity and extinction risk in birds, focusing on contemporary threat status and latent extinction risk. We find that more diverse assemblages have lower mean IUCN threat status despite being composed of species with attributes that make them more vulnerable to extinction, such as large body size or small range size. Indeed, the reduction in current threat status associated with greater diversity far outweighs the increased risk associated with the accumulation of extinction-prone species in more diverse assemblages. Our results suggest that high diversity reduces extinction risk, and that species conservation targets may therefore best be achieved by maintaining high levels of overall biodiversity in natural ecosystems.

KEYWORDS
biodiversity, bird traits, conservation status, extinction risk, macroecology

INTRODUCTION

Numerous experimental and observational studies have shown that biodiversity is positively associated with an array of ecosystem functions (Cardinale et al., 2002, 2006; Emmett Duffy et al., 2017). Increasingly, research on biodiversity–ecosystem function (BEF) relationships is revealing that diversity-driven increases in function can boost rates at which nutrients, energy and organic matter flow through an ecosystem (Cardinale et al., 2012; Emmett Duffy et al., 2017), as well as increasing its overall multifunctionality (Soliveres et al., 2016), stability (Tilman et al., 2014) and resilience (Oliver et al., 2015). In addition, increased diversity is associated with reduced rates of species invasion (Byun et al., 2013; Fargione & Tilman, 2005; Levine et al., 2004; Naeem et al., 2000) and lower rates of disease transmission (Becker et al., 2014). These benefits are generally conceptualised at the scale of whole ecosystems, yet it is also possible that they influence the fate of individual lineages by reducing extinction risk (Weeks et al., 2016b). However, the relationship between the diversity of an assemblage and the risk of

extinction for its constituent lineages is rarely investigated and remains poorly understood.

A key hindrance to progress is that this question is unlikely to be resolved when biodiversity is measured simply in terms of species richness (i.e. taxonomic diversity). Extinction risk may be more closely associated with other aspects of ecosystems, including functional and phylogenetic components of biodiversity (Naeem et al., 2016). For example, functional traits often improve or even outperform estimates based on species richness when predicting ecosystem function and stability (Hooper et al., 2005; Morelli et al., 2020; Tilman et al., 1997), suggesting that extinction risk may be sensitive to variation in functional diversity. Accounting for multidimensionality is also important because different facets of biodiversity can have contrasting responses to environmental change (Chapman et al., 2018) and vary in their predicted relationships with ecosystem function, as well as the mechanisms underpinning those relationships (Flynn et al., 2011; Soliveres et al., 2016). Integrating functional information based on species traits and phylogenetic relationships is particularly important at large

spatial scales where ecological communities are complex and dynamic (Brose & Hillebrand, 2016). As yet, it has proved very difficult to account for such factors in a global context because the necessary combination of species-level information on geographical distributions, phylogenetic relationships and detailed functional traits have not generally been available at sufficiently large spatial and taxonomic scales (Naeem et al., 2016).

Capitalising on the availability of comprehensive phylogenetic (Jetz et al., 2012) and distributional data for birds (BirdLife International, 2015), we develop a multidimensional metric of avian diversity to explore its association with extinction risk at a global scale (measured in terms of contemporary threat status and latent extinction risk). Birds offer an ideal system for this approach because they are distributed worldwide with high quality species-level information on co-occurrence, threat status and—increasingly—functional traits (Tobias et al., 2020). Using a newly compiled data set of morphological trait measurements from >10,000 species, representing >99% of bird species diversity (Pigot et al., 2020), we calculate functional richness (Villéger et al., 2008) for avian assemblages based on body mass, beak shape, leg length and tail length. Recently, analyses confirm that these traits provide a powerful index of avian dietary niche and foraging behaviour (Pigot et al., 2020). Our estimation of functional richness therefore focuses on 'effect traits' (i.e. traits that determine the contribution of an individual to ecosystem functioning; Winemiller et al., 2015).

Since eco-morphological and life history traits are also linked to conservation status in birds (Tobias & Pigot, 2019), we use them to develop a metric of extinction risk. We assume that increases in body mass and ecological specialisation, as well as decreases in dispersal ability, are associated with the increased likelihood that a lineage will go extinct per unit time, as reported in numerous studies (e.g., Bennett & Owens, 1997; Lee & Jetz, 2011; Reinhardt et al., 2005). Because these attributes predict the probability that a species will go extinct, we use our trait-based metric of extinction risk to calculate the collective vulnerability of species in assemblages, or 'assemblage vulnerability' (Weeks et al., 2016b). In other words, assemblages composed of species with low dispersal abilities, large body sizes and high levels of ecological specialisation have greater overall vulnerability. Since our calculation of assemblage vulnerability is partly based on the presence of species not currently considered threatened with extinction, but likely to become threatened in the future, it provides a measure of latent extinction risk (i.e., the difference between a species' contemporary extinction risk, and the expected level of risk, given its biology; Cardillo et al., 2006).

Although they can theoretically capture collective or latent extinction risk, trait-based metrics provide a relatively crude estimate of contemporary extinction risk (Tobias & Pigot, 2019). Thus, we also characterise the contemporary extinction risk of assemblages using IUCN Red List status (BirdLife International, 2015). IUCN status is an indicator of current conservation priorities, widely used as an index of relative probabilities of extinction among species (Isaac et al., 2007), or as estimates of instantaneous rates of progression towards extinction (Mooers et al., 2008). Accordingly, we estimate the contemporary extinction risk for an assemblage based on the harmonic mean of the IUCN status (i.e. 'contemporary threat status') of its constituent species. Previous studies have shown that IUCN Red List status and trait-based predictors of extinction risk are correlated in birds (Tobias & Pigot, 2019), but it is less clear how they are linked to biodiversity. Although the standard prediction based on BEF literature is that biodiversity enhances ecosystem functioning, thereby reducing extinction risk, other factors may complicate the outcome. In particular, if occurrence within diverse assemblages reduces rates of extinction for individual lineages, this may—paradoxically—increase assemblage vulnerability through the survival and accumulation of extinction-prone species (Weeks et al., 2016b; Figure 1). These contrasting possibilities set up a potential trade-off whereby increased diversity may have both positive and negative implications from the perspective of biological conservation.

Integrating taxonomic, phylogenetic and functional diversity metrics, we examine the effects of bird diversity on assemblage vulnerability and IUCN threat status (Figure 2). We use structural equation modelling to quantify the strength of the relationships between bird diversity, assemblage vulnerability and contemporary extinction risk, while controlling for anthropogenic drivers of extinction as well as large-scale gradients in environmental variables and range size. The findings allow us to disentangle the positive and negative effects of biodiversity on contemporary and latent extinction risk, with implications for the prioritisation of conservation interventions.

MATERIALS AND METHODS

Presence–absence matrix

To generate terrestrial bird assemblages, we used a standard 110-km^2 resolution grid, roughly equivalent to 1° latitude and 1° longitude at the equator. We excluded all non-terrestrial cells (those that were >50% ocean or >70% inland water) and all cells below 60° S to remove Antarctica, where the avifauna does not include land birds. We determined species composition of these equal-area-projection cells using species range maps at a 10 km^2 resolution, obtained from BirdLife International. Species can contribute to local ecological dynamics regardless of whether they are resident, breeding or
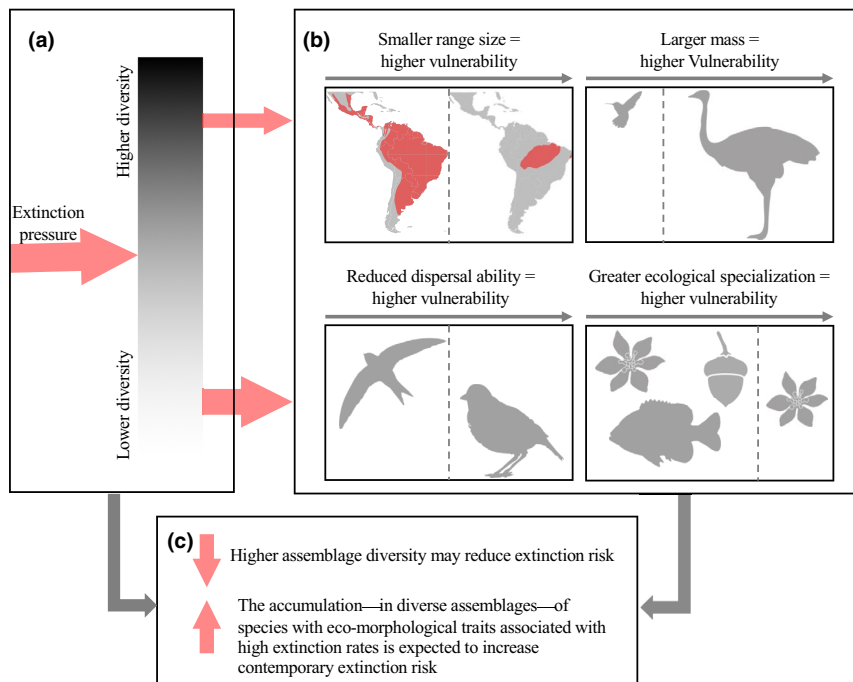
FIGURE 1 Conceptual illustration of the relationship between diversity and extinction risk. (a) Species in more diverse assemblages are hypothesized to have reduced exposure to extinction pressure as a result of biodiversity effects on ecosystem functioning and stability. (b) The phenotypic and biogeographic attributes of individual species in an assemblage determine the impacts of the extinction pressures to which they are exposed (i.e. their vulnerability). (c) Together, the diversity and attributes of constituent species within an assemblage determine the contemporary extinction risk of assemblages. Thus, the relationship between diversity and extinction risk may depend on a trade-off between two inter-dependent processes: 1) the reduction of extinction risk associated with higher assemblage diversity (a→c), and 2) the consequent accumulation of vulnerable species in more diverse assemblages (a→b→c)

non-breeding visitors, therefore we included resident, breeding and non-breeding portions of species ranges when calculating assemblages. Species ranges were trimmed to exclude areas where presence was classified as uncertain or extinct. We also omitted areas where species origin was classified as vagrant, uncertain or invasive, and where seasonality was classified as passage (i.e. only occurring on migration) or uncertain. Any cells with fewer than seven species were removed, so that each cell had enough taxa to calculate the functional richness using six traits (Villéger et al., 2008).

While species occurring in the same grid cell do not necessarily interact as a community, the total avian assemblage we calculate for each cell serves as an estimate of the complete range of traits and trophic interactions that could potentially contribute to ecological functions with relevance to extinction risk. At global scales, quantification and validation of interspecific interactions is not feasible, so co-occurrence within grid cells is routinely used as a proxy for coexistence (e.g. Pigot et al., 2016) or to link biodiversity and ecosystem function (e.g. Duchenne et al., 2020).

Assemblage diversity metrics

To allow phylogenetic analysis, we based our species taxonomy on that used in the global bird phylogeny (www.

birdtree.org; Jetz et al., 2012). For each assemblage occupying each grid cell, we calculated species richness, two measures of phylogenetic diversity, and one metric of functional diversity (Figure 2). Functional diversity was characterised using six ecologically important functional effect traits (total beak length, beak tip to the anterior edge of the nares, beak width, beak depth, tail length and tarsus length) measured on museum specimens (Pigot et al., 2020). For each assemblage, we used these traits to calculate functional richness—the volume of the convex hull that bounds the functional trait space (Villéger et al., 2008)—using the 'dbfd' function in the FD package in R (Laliberté & Legendre, 2010; Laliberté et al. 2015; R Core Team, 2018; see Supporting Informatin for additional detail). All traits were standardised to a mean of zero and standard deviation of one prior to analysis.

In the 'picante' package in R (Kembel et al., 2010), we used the 'pd' and 'cophenetic' functions, respectively, to calculate the phylogenetic diversity of each assemblage as (1) the sum of the branch lengths connecting all species in the community—that is, Faith's phylogenetic diversity index (Faith, 1992)—and (2) the mean pairwise phylogenetic distance (Webb et al., 2002) between all species in the community. The phylogenetic relationships among species were estimated using 1,000 phylogenies taken from the posterior distribution of the Jetz et al., (2012) global phylogeny of birds, with the Hackett et al., (2008)
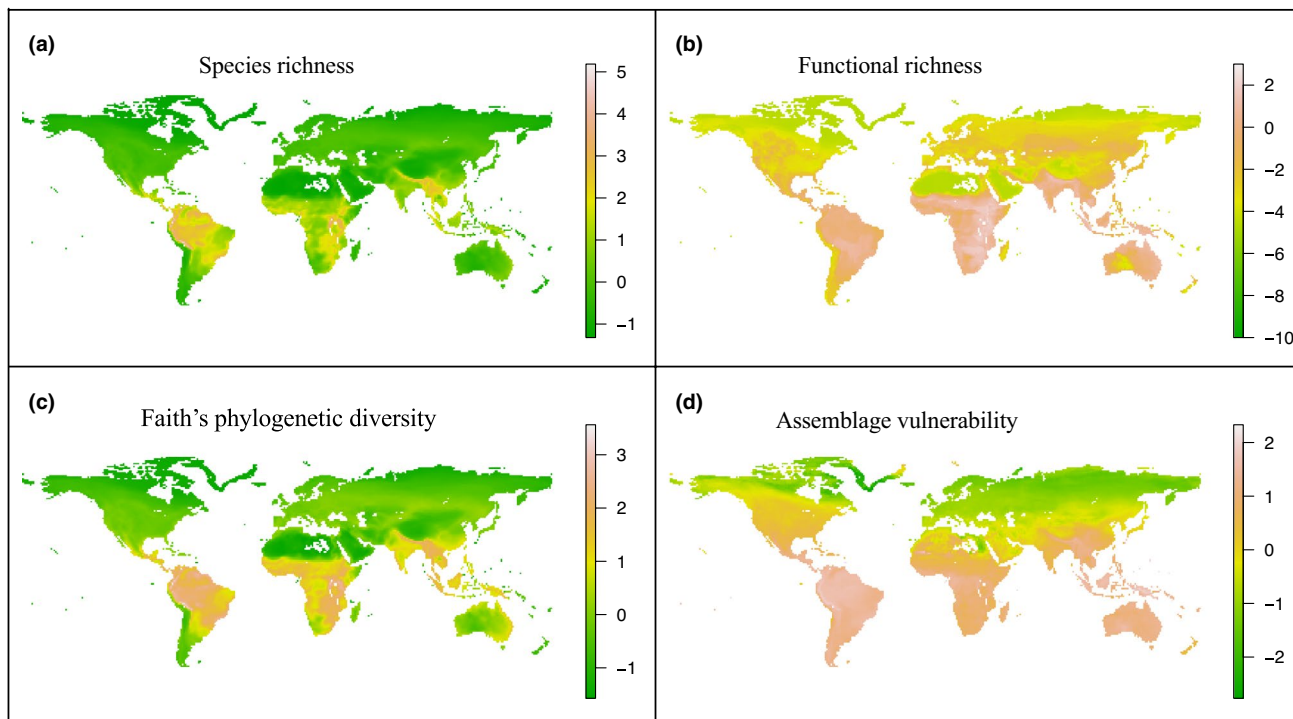
FIGURE 2 Relationship between bird diversity and assemblage vulnerability mapped at global scales. Patterns shown are based on estimates of (a) taxonomic, (b) functional and (c) phylogenetic diversity calculated from all species mapped as occurring in 1 degree grid cells worldwide. Functional diversity is estimated from morphological traits for over 10,000 bird species. We also estimate global variation in (d) assemblage vulnerability (a metric of mean vulnerability to extinction for species in an assemblage), based on biogeographic, ecological and morphological attributes of all species occurring in each grid cell. Maps show each variable standardized to a mean of 0 and standard deviation of 1; the logarithm of standardized functional richness estimates that were transformed to be positive are mapped

phylogeny used as a backbone. Because our models are relatively robust to phylogenetic error, we included those species that did not have genetic data and were placed in the tree by Jetz et al., (2012) using a taxonomic algorithm. From these phylogenies, we calculated a maximum credibility clade tree using DendroPy (Sukumaran & Holder, 2010) as described in Rubolini et al., (2015).

Assemblage vulnerability

To calculate the accumulation of species with traits and distributions that make them pre-disposed to extinction, we quantified assemblage vulnerability for each assemblage in the world, based on a modification of the approach taken by Weeks et al., (2016b). All variables were standardised to a mean of zero and standard deviation of one prior to calculation of vulnerability for both species and assemblages. For each species in an assemblage, we calculated a species-specific vulnerability score (V_s, Equation 1) based on body mass, dispersal ability and ecological specialisation. Body mass was extracted from Tobias and Pigot (2019); dispersal ability was estimated by hand-wing index (Claramunt et al., 2012) with data from Sheard et al., (2020); ecological specialisation was estimated by the trophic diversity of species diets (Pigot et al., 2020; Wilman et al., 2014).

Because dispersal ability is expected to be negatively related to extinction risk (Tobias & Pigot, 2019), we multiply this variable by −1 when incorporating it into V_s:

$$V_s = (\text{Mass} - \text{Hand} - \text{wing Index} + \text{Ecological Specialisation}) - 3 \quad (1)$$

We then calculated the assemblage vulnerability for each assemblage, 'i', as the unweighted arithmetic mean of the vulnerability scores (V_s) for all (n) species in an assemblage:

$$V_{ai} = \left(V_{s1} + V_{s2} .... V_{sn} \right) / n \quad (2)$$

Thus, larger species with low dispersal abilities and greater ecological specialisation would have higher species vulnerability (V_s) scores, and assemblages that are composed of species that tended to have higher V_s scores would have higher assemblage vulnerability (V_a) scores.

Contemporary threat status

To characterise the contemporary threat status of each assemblage, we converted the IUCN threat status of all species to numeric variables (from Least Concern =1 to Critically Endangered =5). For each assemblage, we then calculated the harmonic mean IUCN threat status of its

constituent species. The conversion of IUCN threat status into numeric data can have significant impacts on the estimated relative extinction risk of species (Mooers et al., 2008). Therefore, we test the robustness of our results to our treatment of IUCN ranks by quantifying contemporary threat status as the arithmetic mean of IUCN status – that is, treating IUCN status as an index of the probability of extinction for a species (Isaac et al., 2007) rather than an instantaneous extinction rate (Supporting Information). Prior to modelling, we standardised the assemblage-level variable to have a mean of 0 and a standard deviation of 1, to improve model fitting.

Geographical and environmental variables

We included assemblage latitude in our models as a predictor of diversity, assemblage vulnerability and contemporary threat status because avian diversity varies latitudinally in parallel with numerous other factors (Mittelbach et al., 2007), including all variables underlying the assemblage vulnerability index: body mass (Bergmann's rule), dispersal ability (Sheard et al., 2020) and ecological specialisation (Belmaker et al., 2012). We calculated latitude for each assemblage as the distance between the midpoint of each grid cell and the equator (i.e., the absolute value of the latitude of an assemblage). By including latitude, we also partially control for large-scale gradients in temperature, productivity and geographical range size of birds (Rapoport's rule). However, while latitude explains most variation in temperature, it explains less variation in productivity and range size, both of which may covary with diversity and influence extinction risk at large scales (Jetz & Freckleton, 2015; Tobias & Pigot, 2019). Therefore, we include estimates of productivity and average range size as separate covariates when modelling the relationships between diversity and both contemporary extinction risk and assemblage vulnerability. We calculated the mean net primary productivity (NPP) of each grid cell (Imhoff & Bounoua, 2006) and the average range size for species occurring in each assemblage, where the range size for each species is estimated by the number of grid cells overlapped by the geographical range (Orme et al., 2006).

Structural equation modelling

To explore the relationship between diversity, assemblage vulnerability and contemporary threat status, we fit a structural equation model (SEM) that regressed (1) assemblage vulnerability onto diversity, while controlling for latitude, NPP, and the mean range size of each assemblage's constituent taxa, and (2) contemporary threat status onto diversity and assemblage vulnerability while controlling for latitude, NPP, mean range size and also anthropogenic pressure (Figure 3).

We included anthropogenic pressures on species and habitats as these may influence the relationship between diversity and extinction risk. To do this, we resampled the Human Footprint Index (Venter et al., 2016) – a widely used metric of human population pressure and land use modification, normalised by biome – to match the spatial resolution of our diversity data using bilinear interpolation conducted in ArcGIS, a common resampling technique that adjusts the resolution of spatial data using the distance-weighted average of the four nearest pixels to a given point (Chang, 2008). This allowed us to incorporate the Human Footprint Index into our analyses as a predictor of contemporary threat status.

In our model, we characterised diversity as a latent variable reflected in the observed (i.e. exogenous, as opposed to latent) covariates: species richness, functional richness, Faith's phylogenetic diversity and mean pairwise phylogenetic distance measures of the species in an assemblage (Figure 3). This approach is based on the conceptual framework of Naeem et al., (2016), in which diversity is treated as a multidimensional construct, with each exogenous predictor measured as described in the *Community Diversity Metrics* section, above. The loading of functional richness on diversity was set to 1 to constrain the scale of the latent diversity variable (Rosseel, 2012).

Each path coefficient linking two variables in our SEM (Figure 3) was considered to be the direct effect of the predictor variable on the response. The indirect effect of diversity on contemporary threat status (via the effect of diversity on assemblage vulnerability) was calculated as the product of the path coefficient linking diversity and assemblage vulnerability and the path coefficient linking assemblage vulnerability and contemporary threat status. All reported coefficients are standardised.

To account for the potential impacts of spatial autocorrelation, we fit the SEM using a flexible approach that permits the comparison of non-spatial and spatially explicit SEMs (Lamb et al., 2014; Rosseel, 2012). We compared a non-spatial SEM and two spatial SEMs that included one or two spatial bins for the data, with a lag distance upper limit of 10% of the total distance between points. Models were fit using the 'runModels' function from the SESEM package in R (Lamb et al., 2014; R Core Team, 2018) and a distance matrix that was generated using the great circle distances among assemblages calculated using the 'rdist.earth' function in the fields package in R (Nychka et al., 2017). We compared model fit using the Akaike's information criterion (AIC) and the comparative fit index (CFI). We report model statistics, parameters and parameter significance estimates from the best-fitting SEM.

RESULTS

We characterised functional, phylogenetic and taxonomic diversity for 16,468 avian assemblages worldwide

FIGURE 3 Results of the structural equation model showing links between different components of diversity (top row) and extinction risk (middle row) while controlling for a range of covariates (bottom row). Black arrows indicate positive relationships; green arrows indicate negative relationships. All relationships are significant and the width of the arrows is scaled to standardized effect size; model coefficients for key relationships are noted (Table S1). Arrows connecting diversity to univariate dimensions represent the loadings of diversity on each dimension. Arrows connecting diversity, assemblage vulnerability, contemporary threat status, human footprint, latitude, NPP and range size represent regression parameters connecting the predictor to response variables. Apparent positive relationship between range size and contemporary threat status is driven by the high correlation between range size and latitude (see Supporting Information). Greater diversity is associated with lower contemporary threat status, even after accounting for the increased assemblage vulnerability associated with greater diversity

(Figure 2). The best-fitting model was a non-spatial model, although spatially explicit models resulted in qualitatively similar relationships (Supporting Information; Tables S1 and S2). While metrics of the absolute goodness of fit were relatively low (RMSEA $= 0.18$; $\chi^2 = 1,2413$, df $= 23$, $p < 0.01$), this is not particularly surprising given the scope of the dataset, the simplicity of the model, and the tendency for ecological data to be noisy. More importantly, the model fit the data well compared to a null model (CFI $= 0.88$).

In our model, the latent diversity variable had positive loadings on all exogenous predictors of diversity: species richness ($\beta = 0.96$, $p < 0.01$), functional richness ($\beta = 0.66$), Faith's phylogenetic diversity ($\beta = 1.02$, $p < 0.01$) and mean pairwise phylogenetic distance ($\beta = 0.09$, $p < 0.01$). We found that diversity was positively associated with NPP ($\beta = 0.54$, $p < 0.01$) and negatively associated with latitude ($\beta = -0.35$, $p < 0.01$), in line with the latitudinal diversity gradient (Mittelbach et al., 2007).

Similarly, assemblage vulnerability was positively associated with NPP ($\beta = 0.10$, $p < 0.01$) and negatively associated with latitude ($\beta = -0.42$, $p < 0.01$). Average range

size was negatively associated with assemblage vulnerability ($\beta = -0.17$, $p < 0.01$). After accounting for these environmental and biogeographic variables, we found that diversity was significantly positively associated with assemblage vulnerability ($\beta = 0.16$, $p < 0.01$), suggesting that more diverse assemblages tend to be characterised by more vulnerable species. The model explained a substantial proportion of the overall variance in assemblage vulnerability ($R^2 = 0.55$).

As with assemblage vulnerability, contemporary threat status (i.e. mean IUCN threat level) was negatively associated with latitude ($\beta = -0.23$, $p < 0.01$) and weakly positively associated with NPP ($\beta = 0.05$, $p < 0.01$). The Human Footprint Index was significantly positively associated with contemporary threat status ($\beta = 0.05$ $p < 0.01$), indicating that areas with higher levels of human modification of the environment support assemblages with higher contemporary threat status. Average range size was significantly positively associated with contemporary threat status ($\beta = 0.03$, $p < 0.01$), which at first glance is counter-intuitive because small range size is a key criterion for assigning IUCN threat

status. However, the relationship was very weak and appears to be explained by the high correlation between range size and latitude (0.69; Rapoport's Rule). A more intuitive negative relationship between average range size and contemporary threat status is found when latitude is removed as a predictor of contemporary threat status (Supporting Information). After accounting for these factors, we found that diversity is significantly negatively associated with contemporary threat status ($\beta = -0.42$, $p < 0.01$), suggesting that more diverse assemblages had lower mean IUCN threat level; notably, the effect of diversity on contemporary threat status was stronger than any of the environmental variables. Assemblage vulnerability was positively associated with contemporary threat status, but the effect size was relatively small ($\beta = 0.07$, $p < 0.01$). The model explained 9% of the variance in contemporary threat status.

Overall, while diversity had a significant negative direct effect on contemporary threat status ($\beta = -0.42$), it had a contrasting positive indirect effect on contemporary threat status ($\beta = 0.01$; Figure 3). This indirect increase in contemporary threat, driven by the accumulation of more vulnerable species in more diverse assemblages, may partly limit the benefit of diversity in reducing contemporary threats, although the beneficial effect is much larger.

DISCUSSION

By compiling multiple dimensions of diversity data for the global avifauna, we have shown that species occurring in assemblages with higher levels of diversity have reduced contemporary extinction risk. It may seem intuitive that reduced extinction risk has resulted in increased diversity, particularly over deeper timescales at which declining extinction rates towards the equator have allowed species richness to build up in tropical biota, driving latitudinal diversity gradients (Mittelbach et al., 2007). However, our analyses focus on contemporary and latent extinction risk, a temporal scale less relevant to the effect of diversification or glaciation, and more relevant to the near-term trends determining IUCN Red List status and vulnerability. Recent anthropogenic threats have driven relatively few bird lineages to extinction but have caused a significant proportion of global avian diversity to be classified as threatened (BirdLife International, 2015). At this temporal scale, our results are more likely to be explained by inherent or coincidental characteristics of diverse ecosystems. One plausible explanation, based on the rapidly growing field of BEF research, is that increases across multiple facets of diversity reflect a higher level and stability of ecosystem functioning. This may take the form of more complete networks of species interactions and associated processes, or the buffering effect of biodiversity against risks such as invasion or disease (Becker et al., 2014; Byun et al., 2013; Fargione & Tilman, 2005; Levine et al., 2004; Naeem et al., 2000).

The main alternative explanations for the relationship between diversity and extinction risk involve large-scale correlations between diversity and anthropogenic threats, environmental conditions and species traits, many of which vary with latitude (Mittelbach et al., 2007). We do find evidence that both contemporary extinction risk and assemblage vulnerability are predicted by latitude, NPP and geographic range size, and that the Human Footprint Index is positively associated with contemporary extinction risk. Nonetheless, after accounting for these variables in our models, we find that diversity has a significant effect on both contemporary and latent extinction risk. Indeed, the effect of diversity on contemporary threat status is larger than that of any environmental or anthropogenic variable.

Other factors to consider include geographical biases in data quality. For example, threat status may be underestimated in the most diverse regions because tropical species are less well-known than temperate species. Although this type of information bias could potentially drive an inverse relationship between diversity and extinction risk, it is unlikely to explain our results because the conservation status of birds is relatively well-understood, even in tropical systems (Tobias et al., 2013). In any case, the threat status of poorly known or rarely detected species is perhaps more often overestimated (Tobias et al., 2013), an effect that would run counter to the patterns detected in our analyses.

Our approach relies on IUCN threat status and a set of variables used to determine assemblage vulnerability. Although these metrics and variables are widely considered to be valid indicators of extinction risk, their connection to extinction rate is complicated (Harcourt, 2005). Ecological specialisation might, for example, influence IUCN threat status designations without necessarily being related to extinction rates (Day et al., 2016). As a result, the association we identify between assemblage vulnerability and IUCN status may to some extent be driven by the variables underlying our metric of assemblage vulnerability rather than a causal effect on extinction rate. Nonetheless, we find no evidence that any individual variable underlying our assemblage vulnerability index is particularly important in driving the key relationships we have identified (Supporting Information).

While the direct reduction in contemporary extinction risk associated with diversity suggests that species in more diverse assemblages are at lower risk of extinction, the relationship between diversity and extinction risk is shaped by the dynamic history of community assembly (Weeks et al., 2016a). For example, reduced extinction pressure may result in the long-term survival of species otherwise prone to extinction, which therefore tend to accumulate in diverse assemblages over time (Weeks

et al., 2016b). There is some evidence that this occurs in plants: climatic stability is thought to have reduced extinction risk for rare species, allowing them to persist in climatically stable regions, with the result that climate change and anthropogenic drivers of extinction are now disproportionately impacting rare species in more diverse regions (Enquist et al., 2019).

In accordance with the idea that diversity can both decrease short-term and increase long-term vulnerability, we find that the reduction in contemporary extinction risk associated with higher diversity ($\beta = -0.42$) is coupled with an increase in latent extinction risk, as measured by assemblage vulnerability, in more diverse assemblages ($\beta = 0.15$). This suggests that more diverse assemblages are composed of many species that are not currently categorised as threatened, but with attributes associated with higher risk of extinction: poor dispersal ability, large body size and greater ecological specialisation. One possible interpretation of this pattern is that attributes associated with increased vulnerability may promote diversification (e.g., reduced dispersal ability can lead to increased diversification rates; Weeks & Claramunt, 2014). However, the association between our indices of vulnerability and diversification rates at global scales is weak and mixed (Owens et al., 1999; Tobias et al., 2020), suggesting that their role as drivers of diversification is unlikely to explain our results. Overall, we interpret the elevated vulnerability of diverse assemblages as an outcome of lower rates of extinction for extinction-prone species, suggesting that the long-term consequence of lower extinction risk for species in diverse assemblages is an increase in latent extinction risk.

To understand the overall relationship between biodiversity and extinction risk in natural systems, it is important to disentangle the contrasting effects of diversity on the current survival prospects of individual lineages (reduced short-term risk) from the accumulation of species inherently predisposed to extinction in the future (increased long-term risk). When we assess the relationship between assemblage vulnerability and contemporary extinction risk, we find a weak positive association ($\beta = 0.06$). This result reveals an indirect mechanism by which biodiversity could ultimately increase contemporary extinction risk: more diverse communities accumulate inherently extinction-prone species, boosting the average threat status of community members. However, the increase in contemporary extinction risk via this indirect effect of diversity ($\beta = 0.01$) is an order of magnitude weaker than the direct effect of high diversity in reducing contemporary extinction risk ($\beta = -0.42$). In other words, the effect of diversity in boosting latent extinction risk is negligible in comparison with its direct effect in reducing contemporary extinction risk.

Interpreting relative differences in assemblage-level IUCN status presents non-trivial challenges. If IUCN threat status is considered to be an index of the probability of extinction (e.g., Isaac et al., 2007), different approaches have been shown to result in different relative estimates of risk based on IUCN status (Mooers et al., 2008). Our approach—based on the harmonic mean of the IUCN status of species in an assemblage—assumes that threat status represents an estimate of the instantaneous rate of progress of a species towards extinction (Mooers et al., 2008). Despite the potential for these different treatments to alter relative estimates of extinction probability, we find that treating IUCN status as estimates of probability of extinction (by taking the arithmetic mean of status) or estimates of instantaneous rates (by taking the harmonic mean of status) does not qualitatively change the relationship between diversity and extinction risk (Table S4).

The effects of biodiversity on ecosystem function can be complicated by assembly history (Fukami & Morin, 2003) and temporal scale (Reich et al., 2012). For similar reasons, historical biogeography can alter the relationship between biodiversity and vulnerability (Weeks et al., 2016b). Predicting the effects of future biodiversity loss on ecosystem functioning, and thus threat status, may be further complicated by shifts in the species-specific functioning or abundance of surviving taxa (De Laender et al., 2016). Thus, the balance between diversity-driven reductions in contemporary extinction risk and increases in the number of species inherently sensitive to extinction may be altered according to context, with some diverse communities having higher vulnerability than others as a result of the phenotypic, biogeographic and functional attributes of their constituent species.

Further research is clearly needed to analyse the relationship between diversity and extinction risk in different historical contexts and across a range of spatial and temporal scales, as well as through a more complete characterisation of anthropogenic pressures. Another priority for future studies is to test the effects of diversity on extinction risk at the species level, rather than the assemblage level, as this may increase statistical power and allow a more sophisticated consideration of phylogenetic relationships and biases in knowledge.

CONCLUSIONS

By quantifying spatial variation in multiple dimensions of diversity at a global scale, we show that higher diversity is associated with reduced contemporary extinction risk and increased assemblage vulnerability in birds. It is difficult to pinpoint the exact causes of this general pattern, but it may reflect higher levels of ecosystem functioning in more biodiverse assemblages. This effect may reduce immediate extinction risks in diverse ecosystems while also inflating the number of extinction-prone species that are able to survive. We also show that the reduction of extinction risk associated with increased diversity is far stronger than the contrasting increase in extinction-prone species associated with greater

assemblage vulnerability in these assemblages. We conclude that the maintenance of biodiverse communities may be a cost-effective approach for preventing extinction, reducing the longer-term need for expensive single-species conservation interventions. This finding adds further impetus to calls for the preservation of intact ecosystems (Di Marco et al., 2019) and wilderness areas (Lovejoy, 2016) to ensure that high levels of biodiversity are maintained at regional scales.

AUTHOR CONTRIBUTIONS

BW conceived the study and performed the analyses; JT and SN helped to develop the conceptual framework; JT provided trait data; JL contributed to the analyses; all authors contributed to writing and revising the manuscript.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13860.

DATA AVAILABILITY STATEMENT

Trait data used in this study are published openly in the same volume, all other datasets and custom code are available on Zenodo: https://doi.org/10.5281/zenodo.5139951.

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SUPPORTING INFORMATION

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