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Diversity and extinction risk are inversely related at a global scale

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AUTHOR CONTRIBUTIONS

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

32

33 **DATA AVAILABILITY STATEMENT**

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

36

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49

50 **Abstract**

51 Increases in biodiversity often lead to greater, and less variable, levels of ecosystem
52 functioning. However, whether species are therefore less likely to go extinct in more diverse
53 ecosystems is unclear. We use comprehensive estimates of avian taxonomic, phylogenetic and
54 functional diversity to characterize the global relationship between multiple dimensions of
55 diversity and extinction risk in birds, focusing on contemporary threat status and latent extinction
56 risk. We find that more diverse assemblages have lower mean IUCN threat status despite being
57 composed of species with attributes that make them more vulnerable to extinction, such as large
58 body size or small range size. Indeed, the reduction in current threat status associated with
59 greater diversity far outweighs the increased risk associated with the accumulation of extinction-

60 prone species in more diverse assemblages. Our results suggest that high diversity reduces
61 extinction risk, and that species conservation targets may therefore best be achieved by
62 maintaining high levels of overall biodiversity in natural ecosystems.

63

64 INTRODUCTION

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

79 A key hindrance to progress is that this question is unlikely to be resolved when
80 biodiversity is measured simply in terms of species richness (i.e. taxonomic diversity).
81 Extinction risk may be more closely associated with other aspects of ecosystems, including
82 functional and phylogenetic components of biodiversity (Naeem *et al.* 2016). For example,
83 functional traits often improve or even outperform estimates based on species richness when
84 predicting ecosystem function and stability (Tilman *et al.* 1997; Hooper *et al.* 2005; Morelli *et al.*
85 2020), suggesting that extinction risk may be sensitive to variation in functional diversity.
86 Accounting for multidimensionality is also important because different facets of biodiversity can
87 have contrasting responses to environmental change (Chapman *et al.* 2018) and vary in their
88 predicted relationships with ecosystem function, as well as the mechanisms underpinning those
89 relationships (Flynn *et al.* 2011; Soliveres *et al.* 2016). Integrating functional information based
90 on species traits and phylogenetic relationships is particularly important at large spatial scales

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

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

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

121 difference between a species' contemporary extinction risk, and the expected level of risk, given
122 its biology; Cardillo *et al.* 2006).

123 Although they can theoretically capture collective or latent extinction risk, trait-based
124 metrics provide a relatively crude estimate of contemporary extinction risk (Tobias & Pigot
125 2019). Thus, we also characterize the contemporary extinction risk of assemblages using IUCN
126 Red List status (BirdLife International 2015). IUCN status is an indicator of current conservation
127 priorities, widely used as an index of relative probabilities of extinction among species (Isaac *et*
128 *al.* 2007), or as estimates of instantaneous rates of progression toward extinction (Mooers *et al.*
129 2008). Accordingly, we estimate the contemporary extinction risk for an assemblage based on
130 the harmonic mean of the IUCN status (i.e. 'contemporary threat status') of its constituent
131 species. Previous studies have shown that IUCN Red List status and trait-based predictors of
132 extinction risk are correlated in birds (Tobias & Pigot 2019), but it is less clear how they are
133 linked to biodiversity. Although the standard prediction based on BEF literature is that
134 biodiversity enhances ecosystem functioning, thereby reducing extinction risk, other factors may
135 complicate the outcome. In particular, if occurrence within diverse assemblages reduces rates of
136 extinction for individual lineages, this may—paradoxically—increase assemblage vulnerability
137 through the survival and accumulation of extinction-prone species (Weeks *et al.* 2016b; Fig. 1).
138 These contrasting possibilities set up a potential trade-off whereby increased diversity may have
139 both positive and negative implications from the perspective of biological conservation.

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

148

149 **METHODS**

150 **Presence-absence matrix**

151 To generate terrestrial bird assemblages, we used a standard 110-km² resolution grid,
152 roughly equivalent to 1° latitude and 1° longitude at the equator. We excluded all non-terrestrial
153 cells (those that were > 50% ocean or > 70% inland water) and all cells below 60° S to remove
154 Antarctica, where the avifauna does not include land birds. We determined species composition
155 of these equal-area-projection cells using species range maps at a 10 km² resolution, obtained
156 from BirdLife International. Species can contribute to local ecological dynamics regardless of
157 whether they are resident, breeding or non-breeding visitors, therefore we included resident,
158 breeding and non-breeding portions of species ranges when calculating assemblages. Species
159 ranges were trimmed to exclude areas where presence was classified as uncertain or extinct. We
160 also omitted areas where species origin was classified as vagrant, uncertain or invasive, and
161 where seasonality was classified as passage (i.e. only occurring on migration) or uncertain. Any
162 cells with fewer than 7 species were removed, so that each cell had enough taxa to calculate
163 functional richness using 6 traits (Villéger *et al.* 2008).

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

171

172 **Assemblage diversity metrics**

173 To allow phylogenetic analysis, we based our species taxonomy on that used in the global
174 bird phylogeny (www.birdtree.org; Jetz *et al.* 2012). For each assemblage occupying each grid
175 cell, we calculated species richness, two measures of phylogenetic diversity, and one metric of
176 functional diversity (Fig. 2). Functional diversity was characterized using six ecologically-
177 important functional effect traits (total beak length, beak tip to the anterior edge of the nares,
178 beak width, beak depth, tail length, and tarsus length) measured on museum specimens (Pigot *et al.*
179 *et al.* 2020). For each assemblage, we used these traits to calculate functional richness—the volume
180 of the convex hull that bounds the functional trait space (Villéger *et al.* 2008)—using the ‘dbfd’
181 function in the FD package in R (Laliberté & Legendre 2010; Laliberté *et al.* 2015; R Core Team

182 2018; see Supporting Informatin for additional detail). All traits were standardized to a mean of
183 zero and standard deviation of one prior to analysis.

184 In the ‘picante’ package in R (Kembel *et al.* 2010), we used the ‘pd’ and ‘cophenetic’
185 functions, respectively, to calculate the phylogenetic diversity of each assemblage as (1) the sum
186 of the branch lengths connecting all species in the community—i.e. Faith’s phylogenetic
187 diversity index (Faith 1992)—and (2) the mean pairwise phylogenetic distance (Webb *et al.*
188 2002) between all species in the community. The phylogenetic relationships among species were
189 estimated using 1,000 phylogenies taken from the posterior distribution of the Jetz *et al.* (2012)
190 global phylogeny of birds, with the Hackett *et al.* (2008) phylogeny used as a backbone. Because
191 our models are relatively robust to phylogenetic error, we included those species that did not
192 have genetic data and were placed in the tree by Jetz *et al.* (2012) using a taxonomic algorithm.
193 From these phylogenies, we calculated a maximum credibility clade tree using DendroPy
194 (Sukumaran & Holder 2010) as described in Rubolini *et al.* (2015).

195

196 **Assemblage vulnerability**

197 To calculate the accumulation of species with traits and distributions that make them pre-
198 disposed to extinction, we quantified assemblage vulnerability for each assemblage in the world,
199 based on a modification of the approach taken by Weeks *et al.* (2016b). All variables were
200 standardized to a mean of zero and standard deviation of one prior to calculation of vulnerability
201 for both species and assemblages. For each species in an assemblage, we calculated a species-
202 specific vulnerability score (V_s , eqn 1) based on body mass, dispersal ability and ecological
203 specialization. Body mass was extracted from Tobias & Pigot (2019); dispersal ability was
204 estimated by hand-wing index (Claramunt *et al.* 2012) with data from Sheard *et al.* (2020);
205 ecological specialization was estimated by the trophic diversity of species diets (Wilman *et al.*
206 2014; Pigot *et al.* 2020).

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

$$209 \quad V_s = (\text{Mass} - \text{Hand-wing Index} + \text{Ecological Specialization})/3$$

210 eqn 1

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

213
$$V_{ai} = (V_{s1} + V_{s2} \dots V_{sn})/n$$

214 eqn 2

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

218

219 **Contemporary threat status**

220 To characterize the contemporary threat status of each assemblage, we converted the
221 IUCN threat status of all species to numeric variables (from Least Concern = 1 to Critically
222 Endangered = 5). For each assemblage, we then calculated the harmonic mean IUCN threat
223 status of its constituent species. The conversion of IUCN threat status into numeric data can have
224 significant impacts on the estimated relative extinction risk of species (Mooers *et al.* 2008).
225 Therefore, we test the robustness of our results to our treatment of IUCN ranks by quantifying
226 contemporary threat status as the arithmetic mean of IUCN status – i.e. treating IUCN status as
227 an index of the probability of extinction for a species (Isaac *et al.* 2007) rather than an
228 instantaneous extinction rate (Supporting Information). Prior to modeling, we standardized the
229 assemblage-level variable to have a mean of 0 and a standard deviation of 1, to improve model
230 fitting.

231

232 **Geographic and environmental variables**

233 We included assemblage latitude in our models as a predictor of diversity, assemblage
234 vulnerability and contemporary threat status because avian diversity varies latitudinally in
235 parallel with numerous other factors (Mittelbach *et al.* 2007), including all variables underlying
236 the assemblage vulnerability index: body mass (Bergmann’s rule), dispersal ability (Sheard *et al.*
237 2020) and ecological specialization (Belmaker *et al.* 2012). We calculated latitude for each
238 assemblage as the distance between the midpoint of each grid cell and the equator (i.e., the
239 absolute value of the latitude of an assemblage). By including latitude, we also partially control
240 for large-scale gradients in temperature, productivity and geographical range size of birds
241 (Rapoport’s rule). However, while latitude explains most variation in temperature, it explains
242 less variation in productivity and range size, both of which may covary with diversity and
243 influence extinction risk at large scales (Jetz & Freckleton 2015; Tobias & Pigot 2019).

244 Therefore, we include estimates of productivity and average range size as separate covariates
245 when modeling the relationships between diversity and both contemporary extinction risk and
246 assemblage vulnerability. We calculated the mean net primary productivity (NPP) of each grid
247 cell (Imhoff & Bounoua 2006) and the average range size for species occurring in each
248 assemblage, where the range size for each species is estimated by the number of grid cells
249 overlapped by the geographical range (Orme *et al.* 2006).

250

251 **Structural equation modeling**

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

258 We included anthropogenic pressures on species and habitats as these may influence the
259 relationship between diversity and extinction risk. To do this, we resampled the Human Footprint
260 Index (Venter *et al.* 2016) – a widely used metric of human population pressure and land use
261 modification, normalized by biome – to match the spatial resolution of our diversity data using
262 bilinear interpolation conducted in ArcGIS, a common resampling technique that adjusts the
263 resolution of spatial data using the distance-weighted average of the four nearest pixels to a
264 given point (Chang 2009). This allowed us to incorporate the Human Footprint Index into our
265 analyses as a predictor of contemporary threat status.

266 In our model, we characterized diversity as a latent variable reflected in the observed (i.e.
267 exogenous, as opposed to latent) covariates: species richness, functional richness, Faith's
268 phylogenetic diversity, and mean pairwise phylogenetic distance measures of the species in an
269 assemblage (Fig. 3). This approach is based on the conceptual framework of Naeem *et al.*
270 (2016), in which diversity is treated as a multidimensional construct, with each exogenous
271 predictor measured as described in the *Community Diversity Metrics* section, above. The loading
272 of functional richness on diversity was set to 1 to constrain the scale of the latent diversity
273 variable (Rosseel 2012).

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

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

290

291 RESULTS

292 We characterized functional, phylogenetic, and taxonomic diversity for 16,468 avian
293 assemblages worldwide (Fig. 2). The best-fitting model was a non-spatial model, although
294 spatially explicit models resulted in qualitatively similar relationships (Supporting Information;
295 Tables S1 and S2). While metrics of the absolute goodness of fit were relatively low (RMSEA =
296 0.18; $\chi^2 = 1,2413$, $df = 23$, $P < 0.01$), this is not particularly surprising given the scope of the
297 dataset, the simplicity of the model, and the tendency for ecological data to be noisy. More
298 importantly, the model fit the data well compared to a null model (CFI = 0.88).

299 In our model, the latent diversity variable had positive loadings on all exogenous
300 predictors of diversity: species richness ($\beta = 0.96$, $P < 0.01$), functional richness ($\beta = 0.66$),
301 Faith’s phylogenetic diversity ($\beta = 1.02$, $P < 0.01$), and mean pairwise phylogenetic distance ($\beta =$
302 0.09 , $P < 0.01$). We found that diversity was positively associated with NPP ($\beta = 0.54$, $P < 0.01$)
303 and negatively associated with latitude ($\beta = -0.35$, $P < 0.01$), in line with the latitudinal diversity
304 gradient (Mittelbach *et al.* 2007).

305 Similarly, assemblage vulnerability was positively associated with NPP ($\beta = 0.10, P <$
306 0.01) and negatively associated with latitude ($\beta = -0.42, P < 0.01$). Average range size was
307 negatively associated with assemblage vulnerability ($\beta = -0.17, P < 0.01$). After accounting for
308 these environmental and biogeographic variables, we found that diversity was significantly
309 positively associated with assemblage vulnerability ($\beta = 0.16, P < 0.01$), suggesting that more
310 diverse assemblages tend to be characterized by more vulnerable species. The model explained a
311 substantial proportion of the overall variance in assemblage vulnerability ($R^2 = 0.55$).

312 As with assemblage vulnerability, contemporary threat status (i.e. mean IUCN threat
313 level) was negatively associated with latitude ($\beta = -0.23, P < 0.01$) and weakly positively
314 associated with NPP ($\beta = 0.05, P < 0.01$). The Human Footprint Index was significantly
315 positively associated with contemporary threat status ($\beta = 0.05, P < 0.01$), indicating that areas
316 with higher levels of human modification of the environment support assemblages with higher
317 contemporary threat status. Average range size was significantly positively associated with
318 contemporary threat status ($\beta = 0.03, P < 0.01$), which at first glance is counter-intuitive because
319 small range size is a key criterion for assigning IUCN threat status. However, the relationship
320 was very weak and appears to be explained by the high correlation between range size and
321 latitude (0.69 ; Rapoport's Rule). A more intuitive negative relationship between average range
322 size and contemporary threat status is found when latitude is removed as a predictor of
323 contemporary threat status (Supporting Information). After accounting for these factors, we
324 found that diversity is significantly negatively associated with contemporary threat status ($\beta = -$
325 $0.42, P < 0.01$), suggesting more diverse assemblages had lower mean IUCN threat level;
326 notably, the effect of diversity on contemporary threat status was stronger than any of the
327 environmental variables. Assemblage vulnerability was positively associated with contemporary
328 threat status, but the effect size was relatively small ($\beta = 0.07, P < 0.01$). The model explained
329 9% of the variance in contemporary threat status.

330 Overall, while diversity had a significant negative direct effect on contemporary threat
331 status ($\beta = -0.42$), it had a contrasting positive indirect effect on contemporary threat status ($\beta =$
332 0.01 ; Fig. 3). This indirect increase in contemporary threat, driven by the accumulation of more
333 vulnerable species in more diverse assemblages, may partly limit the benefit of diversity in
334 reducing contemporary threats, although the beneficial effect is much larger.

335

336 **DISCUSSION**

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

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

363 Other factors to consider include geographical biases in data quality. For example, threat
364 status may be underestimated in the most diverse regions because tropical species are less well
365 known than temperate species. Although this type of information bias could potentially drive an
366 inverse relationship between diversity and extinction risk, it is unlikely to explain our results

367 because the conservation status of birds is relatively well understood, even in tropical systems
368 (Tobias *et al.* 2013). In any case, the threat status of poorly known or rarely detected species is
369 perhaps more often overestimated (Tobias *et al.* 2013), an effect that would run counter to the
370 patterns detected in our analyses.

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

381 While the direct reduction in contemporary extinction risk associated with diversity
382 suggests that species in more diverse assemblages are at lower risk of extinction, the relationship
383 between diversity and extinction risk is shaped by the dynamic history of community assembly
384 (Weeks *et al.* 2016a). For example, reduced extinction pressure may result in the long-term
385 survival of species otherwise prone to extinction, which therefore tend to accumulate in diverse
386 assemblages over time (Weeks *et al.* 2016b). There is some evidence that this occurs in plants:
387 climatic stability is thought to have reduced extinction risk for rare species, allowing them to
388 persist in climatically stable regions, with the result that climate change and anthropogenic
389 drivers of extinction are now disproportionately impacting rare species in more diverse regions
390 (Enquist *et al.* 2019).

391 In accordance with the idea that diversity can both decrease short-term and increase long-
392 term vulnerability, we find that the reduction in contemporary extinction risk associated with
393 higher diversity ($\beta = -0.42$) is coupled with an increase in latent extinction risk, as measured by
394 assemblage vulnerability, in more diverse assemblages ($\beta = 0.15$). This suggests that more
395 diverse assemblages are composed of many species that are not currently categorized as
396 threatened, but with attributes associated with higher risk of extinction: poor dispersal ability,
397 large body size, and greater ecological specialization. One possible interpretation of this pattern

398 is that attributes associated with increased vulnerability may promote diversification (e.g.,
399 reduced dispersal ability can lead to increased diversification rates; Weeks & Claramunt 2014).
400 However, the association between our indices of vulnerability and diversification rates at global
401 scales is weak and mixed (Owens *et al.* 1999; Tobias *et al.* 2020), suggesting that their role as
402 drivers of diversification is unlikely to explain our results. Overall, we interpret the elevated
403 vulnerability of diverse assemblages as an outcome of lower rates of extinction for extinction-
404 prone species, suggesting that the long-term consequence of lower extinction risk for species in
405 diverse assemblages is an increase in latent extinction risk.

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

419 Interpreting relative differences in assemblage-level IUCN status presents non-trivial
420 challenges. If IUCN threat status is considered to be an index of the probability of extinction
421 (e.g., Isaac *et al.* 2007), different approaches have been shown to result in different relative
422 estimates of risk based on IUCN status (Mooers *et al.* 2008). Our approach—based on the
423 harmonic mean of the IUCN status of species in an assemblage—assumes that threat status
424 represents an estimate of the instantaneous rate of progress of a species toward extinction
425 (Mooers *et al.* 2008). Despite the potential for these different treatments to alter relative
426 estimates of extinction probability, we find that treating IUCN status as estimates of probability
427 of extinction (by taking the arithmetic mean of status) or estimates of instantaneous rates (by

428 taking the harmonic mean of status) does not qualitatively change the relationship between
429 diversity and extinction risk (Table S4).

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

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

446

447 **CONCLUSIONS**

448 By quantifying spatial variation in multiple dimensions of diversity at a global scale, we
449 show that higher diversity is associated with reduced contemporary extinction risk and increased
450 assemblage vulnerability in birds. It is difficult to pinpoint the exact causes of this general
451 pattern, but it may reflect higher levels of ecosystem functioning in more biodiverse
452 assemblages. This effect may reduce immediate extinction risks in diverse ecosystems while also
453 inflating the number of extinction-prone species that are able to survive. We also show that the
454 reduction of extinction risk associated with increased diversity is far stronger than the contrasting
455 increase in extinction-prone species associated with greater assemblage vulnerability in these
456 assemblages. We conclude that the maintenance of biodiverse communities may be a cost-
457 effective approach to preventing extinction, reducing the longer-term need for expensive single-
458 species conservation interventions. This finding adds further impetus to calls for the preservation

459 of intact ecosystems (Di Marco *et al.* 2019) and wilderness areas (Lovejoy 2016) to ensure that
460 high levels of biodiversity are maintained at regional scales.

461

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466

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632

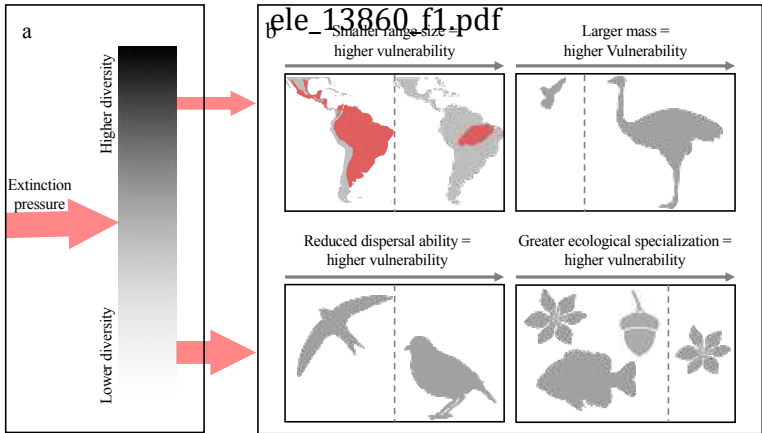
633 **Figure 1.** Conceptual illustration of the relationship between diversity and extinction risk. (a)
634 Species in more diverse assemblages are hypothesized to have reduced exposure to extinction
635 pressure as a result of biodiversity effects on ecosystem functioning and stability. (b) The
636 phenotypic and biogeographic attributes of individual species in an assemblage determine the
637 impacts of the extinction pressures to which they are exposed (i.e. their vulnerability). (c)
638 Together, the diversity and attributes of constituent species within an assemblage determine the
639 contemporary extinction risk of assemblages. Thus, the relationship between diversity and
640 extinction risk may depend on a trade-off between two inter-dependent processes: 1) the
641 reduction of extinction risk associated with higher assemblage diversity (a→c), and 2) the
642 consequent accumulation of vulnerable species in more diverse assemblages (a→b→c).

643

644 **Figure 2.** Relationship between bird diversity and assemblage vulnerability mapped at global
645 scales. Patterns shown are based on estimates of (a) taxonomic, (b) functional, and (c)
646 phylogenetic diversity calculated from all species mapped as occurring in 1 degree grid cells
647 worldwide. Functional diversity is estimated from morphological traits for over 10,000 bird
648 species. We also estimate global variation in (d) assemblage vulnerability (a metric of mean
649 vulnerability to extinction for species in an assemblage), based on biogeographic, ecological and
650 morphological attributes of all species occurring in each grid cell. Maps show each variable
651 standardized to a mean of 0 and standard deviation of 1; the logarithm of standardized functional
652 richness estimates that were transformed to be positive are mapped.

653

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



c

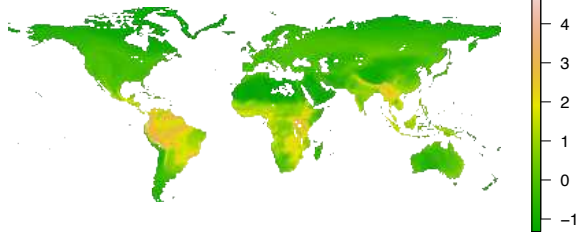
Higher assemblage diversity may reduce extinction risk

The accumulation—in diverse assemblages—of species with eco-morphological traits associated with high extinction rates is expected to increase contemporary extinction risk

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(a)

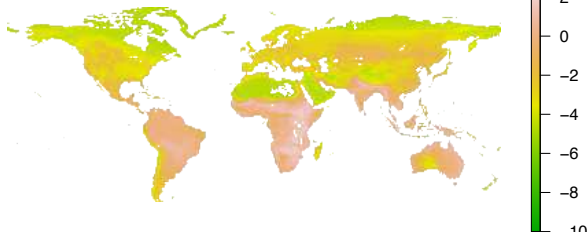
Species richness



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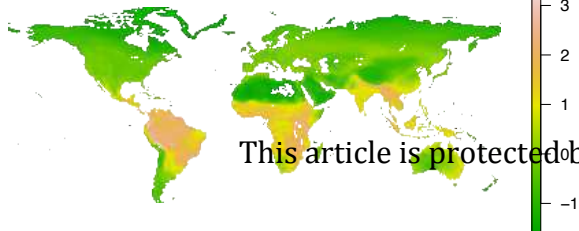
(b)

Functional richness



(c)

Faith's phylogenetic diversity



(d)

Assemblage vulnerability



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Diversity

Extinction Risk

Covariates

