

1 **New species discoveries redefine global biodiversity patterns**

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17

18 **Abstract**

19 Global biodiversity patterns are fundamental to ecology and conservation. However, these patterns are based  
20 on incomplete and rapidly growing taxonomic knowledge, and the influence of new species discoveries on our  
21 understanding of global biodiversity remains poorly understood. Here we quantified how the discovery of  
22 terrestrial vertebrates from 1920 to 2020 has reshaped estimated global diversity patterns and their inferred  
23 environmental drivers. New species discoveries were overwhelmingly concentrated in the tropics. For well-  
24 studied taxa such as birds, estimated diversity patterns remained largely stable, but reptiles and amphibians  
25 showed major reconfiguration: 20.3% and 31.7% of their respective diversity centers (top 5% of range-  
26 weighted rarity) shifted to new regions, including parts of Australia and Southeast Asia. These  
27 reconfigurations were accompanied by marked changes in inferred environmental drivers, with the apparent  
28 influence of temperature on richness declining and precipitation gaining importance. Our findings suggest that  
29 estimated global diversity patterns and driver relationships for poorly studied groups may be less reliable than  
30 often assumed. Consequently, projections of biodiversity change that rely mainly on temperature risk  
31 compromising conservation strategies. Our study calls for “more boots on the ground” to accelerate species  
32 discoveries and close critical biodiversity knowledge gaps.

33

## 34 **Introduction**

35 Understanding global biodiversity patterns and their environmental drivers is crucial in quantifying ecological  
36 and evolutionary processes, identifying conservation priorities, and informing strategies to mitigate biodiversity  
37 losses<sup>1,2</sup>. Global biodiversity has been extensively mapped for well-studied groups such as vertebrates<sup>3-5</sup> and  
38 plants<sup>6,7</sup>, and increasingly for underrepresented taxa like invertebrates<sup>8-10</sup> and microorganisms<sup>11</sup>. However,  
39 these maps often suffer from inherent biases, stemming from uneven geographic coverage and incomplete  
40 taxonomic knowledge<sup>12,13</sup>. These limitations can bias biodiversity assessment, distort ecological and  
41 evolutionary inferences, and lead to suboptimal conservation decisions<sup>14,15</sup>. While geographic biases are  
42 increasingly recognized and addressed<sup>16,17</sup>, the quantitative influences of incomplete taxonomic knowledge,  
43 which is a fundamental limitation known as the Linnean shortfall<sup>18</sup>, on our understanding of global biodiversity  
44 remain largely unknown.

45

46 All taxonomic groups contain a substantial proportion of undiscovered species, with significant new  
47 discoveries in recent decades<sup>19,20</sup>. For example, while over 2,000 new vascular plant species are discovered  
48 annually<sup>21</sup>, it is estimated as many as 100,000 species remain unknown<sup>22</sup>. This trend is also observed in well-  
49 studied taxonomic groups<sup>23</sup>. Between 1993 and 2008, 408 new mammal species were described, accounting  
50 for about 10% of previously known diversity<sup>24,25</sup>. Moreover, undiscovered and newly discovered species are  
51 disproportionately concentrated in biodiversity hotspots and remote areas<sup>26,27</sup>. Incomplete sampling in these  
52 often-inaccessible areas introduces substantial uncertainty into assessments of global biodiversity patterns,  
53 particularly for understudied taxonomic groups<sup>28</sup>. For example, the observed mid-latitude peak in global  
54 earthworm diversity likely reflects under-sampling in the tropics relative to well-sampled temperate regions<sup>9</sup>, a  
55 discrepancy increasingly revealed by molecular studies uncovering the hidden earthworm diversity in the  
56 tropics<sup>29</sup>. Similarly, for ants, centers of richness and rarity are expected to shift significantly with greater  
57 sampling efforts<sup>30</sup>. Given that approximately 80% of Earth's species are yet to be formally described<sup>19</sup>, it is  
58 crucial to understand the distribution of species discoveries and their influences on estimated diversity  
59 patterns.

60

61 Species discoveries can also reshape ecological inferences regarding the relationships between diversity and  
62 environmental factors, challenging predictions about how biodiversity responds to global change. For  
63 example, the prevalence of new species discoveries in tropical regions may strengthen species-energy  
64 relationships by highlighting how more individuals of newly discovered species coexist<sup>1</sup>. Specifically, a hump-  
65 shaped relationship between diversity and mean annual temperature may be further evidenced due to the  
66 disproportionately high diversity in regions with high elevation and relatively cool temperature<sup>27</sup>. Conversely,

67 the environmental heterogeneity hypothesis<sup>31</sup> may also gain further importance in explaining global  
68 biodiversity patterns as species discoveries continue to be made across tropical montane regions<sup>25,32</sup>. While  
69 recent studies have suggested climate as the dominant factor in explaining species richness patterns for  
70 different groups<sup>7,33</sup>, the impact of new species discoveries on the relative role of different aspect of climate  
71 remains poorly understood. Addressing this major knowledge gap is critical for refining extinction risk  
72 assessment and informing conservation strategies, especially for data-deficient taxa<sup>34</sup>.

73

74 Here, we used the IUCN Red List of Threatened Species<sup>35</sup>, which includes up-to-date taxonomic and  
75 geographic information covering a broad range of taxa, to quantify how the inclusion of newly discovered  
76 terrestrial vertebrates alters patterns of species richness and rarity, and influences the environmental drivers  
77 that shape such patterns. We focused on terrestrial vertebrates because they are the primary targets of  
78 conservation efforts and represent a gradient of discovery completeness<sup>5,24,36</sup>. While we recognize that  
79 taxonomic changes (such as splitting and lumping) can increase or decrease species numbers independently  
80 of unknown species<sup>37</sup>, our analysis quantified the influence of new discoveries by using species description  
81 dates to construct temporal discovery trends for vertebrates since 1920. This approach allowed us to  
82 disentangle the explicit influence of newly discovered species from the effects of heterogeneous sampling  
83 efforts across temporal and spatial resources. In this study, we addressed the following three key questions:  
84 1) Where are newly discovered species concentrated? 2) To what extent do these discoveries redefine our  
85 understanding of global diversity patterns, such as the latitudinal diversity gradient<sup>16</sup> and diversity centers<sup>2</sup>? 3)  
86 How do new discoveries modify the inferred relationships between measures like species diversity and  
87 environmental drivers, which are essential for predicting the consequences of global change<sup>10</sup>?

88

## 89 **Results**

### 90 **Geographic shifts in diversity patterns**

91 We found that species discovered between 1920 and 2020 cumulatively constituted 39.6% (13,491 of 34,036  
92 species) of total terrestrial vertebrate species, representing 7.7% (832 of 10,856) of birds, 31.7% (1,774 of  
93 5,586) of mammals, 50.7% (5,012 of 9,880) of reptiles, and 76.1% (5,873 of 7,714) of amphibians (Table 1).  
94 Notably, 17.3% of reptiles and 33.0% of amphibians have been discovered since 2000 (Table 1). New species  
95 discoveries were strongly concentrated in the tropics, decreasing sharply towards the poles (Fig. 1).  
96 Therefore, species discoveries of vertebrates, especially for reptiles and amphibians, accentuated the  
97 unimodality of latitudinal diversity gradients (Fig. 1).

98

99 Across our 95-km-resolution grid, the number of species discoveries showed a significant relationship with  
100 species number in 1920 across all vertebrate groups ( $p < 0.001$  for all four groups based on our generalized  
101 additive models; Fig. 2). Birds and amphibians showed a monotonically increasing number of new  
102 discoveries, whereas discoveries of new mammal species have declined in the most species-rich regions  
103 since 1920. Discoveries of reptiles peaked at a moderate level of historical richness and then plateaued. In  
104 particular, mammal discoveries were exceptionally low in the forests and savannas of Lake Victoria Basin in  
105 East Africa (a mammal biodiversity center), while we found disproportionately high number of discoveries in  
106 Papuan montane forests (Fig. 2c), implying shifting centers of mammalian species discovery over the past  
107 century. Australian savannas and shrublands exhibited an unexpectedly high number of new reptile species  
108 (Fig. 2e), increasing Australia's known diversity by 2.5-fold (from 376 species in 1920 to 933 species in 2020;  
109 Supplementary Fig. 1).

110

111 To assess shifts in diversity centers with high biogeographic uniqueness, we identified regions with the top 5%  
112 range-weighted rarity (emphasizing range-restricted species) and classified their dynamics into three  
113 categories: emergent diversity centers (newly identified after increasing taxonomic knowledge), historical  
114 diversity centers (initially identified but no longer significant following species discoveries), and stable diversity  
115 centers (persistent across all discovery scenarios). Newly discovered bird species had negligible effects on  
116 overall diversity patterns (Fig. 2b). However, we observed significant shift in diversity centers for mammals,  
117 with 12.1% of their total area replaced by emergent centers, a result of shrinkage in the Equatorial Afrotropics  
118 and expansion in the Central Andes, Madagascar, and Indonesian islands (Fig. 2d; Supplementary Table 1).  
119 The spatial change in diversity centers was even more pronounced for reptiles and amphibians, with 20.3%  
120 and 31.7% of their respective center areas being replaced (Supplementary Table 1). For reptiles, emergent  
121 centers predominantly appeared in the northern and western Australian savannas and shrublands (Fig. 2f).  
122 For amphibians, key emergent centers included the Andean montane forests and Southeast Asian tropical  
123 forests (Fig. 2h). These trends for mammals, reptiles and amphibians remain striking across different time  
124 periods and diversity metrics, with substantial shifts observed when considering only the past 20 years (4.3%  
125 for mammals, 5.0% for reptiles, 13.6% for amphibians) or species richness centers (11.2% for mammals,  
126 17.4% for reptiles, 27.3% for amphibians; Supplementary Fig. 2-3 & Table 1).

127

## 128 **Discoveries alter inferred drivers**

129 Our analysis revealed contrasting temporal trends in the relationships between species richness and  
130 environment among vertebrate groups and environmental variables from 1920 to 2020 (Fig. 3; Supplementary  
131 Table 2). While the relationships for birds and mammals remained consistent, those for reptile and amphibian

132 species exhibited substantial temporal changes (Fig. 3). Specifically, the dominant association with mean  
133 annual temperature weakened significantly for reptiles ( $z = 2.01$ ,  $p = 0.04$ ) and amphibians ( $z = 3.70$ ,  $p <$   
134  $0.001$ ), as determined by a modified z-test of variable effect size between 1920 and 2020. Similarly, the  
135 influence of annual precipitation on reptile diversity showed a non-significant, yet clear, decline ( $z = 1.58$ ,  $p =$   
136  $0.11$ ). In contrast, the contribution of precipitation-related factors generally increased for amphibian diversity,  
137 with a significant rise in the influences of precipitation seasonality ( $z = 3.45$ ,  $p = 0.001$ ). The association with  
138 elevation range, as a proxy for environmental heterogeneity, strengthened for reptiles ( $z = -3.77$ ,  $p < 0.001$ )  
139 and amphibians ( $z = -7.80$ ,  $p < 0.001$ ). While the influence of temperature and precipitation anomalies since  
140 the Last Glacial Maximum remained largely consistent, precipitation anomalies showed a significant decline  
141 for reptile diversity pattern ( $z = -2.10$ ,  $p = 0.04$ ; Fig. 3, Supplementary Table 2).

142  
143 As diversity-environment relationships can vary among biogeographic realms due to their divergent  
144 histories<sup>38</sup>, we also analyzed these relationships at the realm level. The Ethiopian, Nearctic, and Palearctic  
145 realms exhibited consistent environment-richness associations across all vertebrate groups (Fig. 4). However,  
146 for reptiles and amphibians in the Australian, Neotropical, and Oriental realms, the trends in relationships  
147 between species richness and temperature and precipitation were generally consistent with global patterns  
148 (Fig. 4, Supplementary Table 3).

149

## 150 **Discussion**

### 151 **Geographic shifts in diversity patterns**

152 The ongoing discovery of new species has profound implications for our understanding of global biodiversity,  
153 especially given the taxonomic and spatial biases inherent in these discoveries<sup>13,18,39</sup>. Our findings  
154 demonstrate that new species discoveries can substantially redefine global diversity patterns, particularly for  
155 understudied taxa (e.g., reptiles and amphibians) and less-explored regions (e.g., the tropical mountains). We  
156 show that species discoveries, which are heavily concentrated in the tropics, have steepened the latitudinal  
157 diversity gradient (Fig. 1). Indeed, the tropics not only host a high diversity of life<sup>40</sup>, but are also home to the  
158 majority of the world's new and undiscovered species<sup>41</sup>, such as vertebrates<sup>25,27</sup>, ants<sup>30</sup>, and plants<sup>26</sup>.

159 However, counter to the expectation that high known diversity would correlate with a high number of species  
160 discoveries<sup>26</sup>, our analysis revealed an opposite trend in some important areas (e.g., mammals in the  
161 Equatorial Afrotropics), resulting in a decline in their relative importance as diversity centers. Instead, we  
162 identified several regions as emergent diversity centers, characterized by a disproportionately high number of  
163 newly discovered species (Fig. 2). This finding, which highlights newly identified diversity centers in the North  
164 Australian Savanna and West Australian Shrubland (for reptiles) and in the Amazonian and Southeast Asian

165 Forests (for amphibians), aligns with the concept of “hidden hotspots”<sup>42</sup> (underrecognized biodiverse regions  
166 due to incomplete knowledge) and “shifted hotspots”<sup>43</sup> (where the relative importance of regions as diversity  
167 hotspots changes once better biodiversity knowledge alter the global ranking) and extends their existence to a  
168 broader spatial and taxonomic scales. The identification of emergent centers not only redefines global  
169 biodiversity patterns, but also highlights previously underrecognized regions that now require emergent  
170 conservation attention.

171

172 Our study also revealed the critical role of historical sampling effort in shaping the temporal change of  
173 diversity patterns. We found that biodiversity patterns for well-studied groups (e.g., birds) and well-sampled  
174 regions (e.g., Palaearctic biogeographic realm) remained consistent despite ongoing species discoveries. This  
175 observation is likely a direct consequence of high historical sampling efforts in these areas<sup>8,44</sup>, which have  
176 yielded a limited number of newly discovered species in recent years. Consequently, existing diversity  
177 patterns for these groups and regions are largely consistent<sup>45</sup>. In contrast, the temporal shift in amphibian  
178 diversity patterns in the Brazilian rainforest and Andean cloud forest is largely due to these regions having  
179 been historically under-sampled<sup>46</sup>. This finding highlights the importance of continued exploration and  
180 taxonomic efforts in under-sampled regions and taxonomic groups.

181

## 182 **Discoveries alter inferred drivers**

183 New species discoveries challenge our understanding of the environmental drivers of biodiversity patterns.  
184 We found a significant decline in the importance of mean annual temperature for explaining the number of  
185 ectothermic reptile and amphibian species, likely because new discoveries are skewed toward habitats with  
186 relatively cool temperatures. For example, the Strabomantidae family, which constitute an exceptionally high  
187 proportion of newly described amphibian species (Supplementary Fig. 4 & 5), is often found in cool and humid  
188 habitats, such as the historically underexplored Andean cloud and montane forests<sup>46</sup>. The discovery of  
189 numerous lizard species in deciduous forests also challenges the assumption that members of this group  
190 prefer hot and arid habitats<sup>36</sup>. As ectothermic vertebrates are generally sensitive to temperature<sup>47</sup>, the  
191 discovery of many new species adapted to cool temperatures is critical. Overlooking these species together  
192 with weakened inferences of diversity-energy relationships, could risk neglecting the threats from rising  
193 temperatures, leading to underestimates future biodiversity loss. Moreover, precipitation-related factors have  
194 become increasingly important in inferring amphibian diversity, as most new amphibian species occur in  
195 tropical regions with relatively high rainfall<sup>42,48</sup>. Given increasing climate extreme events and induced  
196 dryness<sup>47,48</sup>, the influences of precipitation and its variability may have more severe consequences on  
197 amphibians than previously thought. Conversely, the strength of inferred association between annual

198 precipitation and reptile diversity has declined over time, driven mainly by discoveries of arid-tolerant lineages  
199 (e.g., lizards) in savanna regions of Australia and the Cerrado<sup>36,43</sup>. The increasing importance of  
200 environmental heterogeneity in shaping reptile and amphibian diversity further supports the need for ongoing  
201 field surveys in mountain and valley areas<sup>27</sup>, particularly in the Neotropical and Oriental realms. Therefore, our  
202 results challenge the robustness of current biodiversity models and projections (e.g., species distribution  
203 models) that rely heavily on climate-richness relationships.

204

## 205 **Implications**

206 Our findings have important implications for global biodiversity conservation. Specifically, we found that a high  
207 proportion of diversity centers for mammals, reptiles, and amphibians have been replaced over the past  
208 century by newly identified centers in previously overlooked regions, yet these new centers are often  
209 threatened by deforestation and associated biodiversity loss<sup>49</sup>. As a result, we may also be underestimating  
210 hidden biodiversity loss in these regions<sup>23</sup>. In addition, since our study focused on vertebrates, which are  
211 relatively well-studied, global diversity patterns and ecological inferences derived from incomplete taxonomic  
212 knowledge may be even less reliable for poorly studied taxa. Indeed, studies on global patterns of earthworms  
213 and fungi, which are less-studied groups, have been criticized for their incomplete taxonomical surveys<sup>9,15</sup>.  
214 Therefore, it becomes more critical to incorporate unknown species into macroecological studies to effectively  
215 assess and guide conservation across different taxonomic groups<sup>34</sup>, highlighting the need to improve  
216 biodiversity monitoring and close knowledge gaps, as emphasized by the Kunming-Montreal Global  
217 Biodiversity Framework. To effectively integrate new species discoveries into conservation management, we  
218 advocate developing new methods to predict the taxonomic and spatial distributions of undiscovered species  
219 (e.g., ref. 27), especially in tropical and montane areas.

220

221 While mean annual temperature has long been widely used in predicting future biodiversity changes under  
222 global warming<sup>47</sup>, the shifting importance of temperature and precipitation we observed implies that  
223 temperature alone is insufficient to accurately predict species losses of ectothermic vertebrates. While  
224 obtaining reliable precipitation data and using it appropriately for future biodiversity predictions remains a  
225 significant challenge<sup>48</sup>, integrating water availability constraints into assessments of climate change is a  
226 necessary step for designing effective protected areas.

227

228 We are aware that the observed temporal changes in global biodiversity patterns may not exclusively reflect  
229 new species discoveries but are also influenced by taxonomic change, such as species lumping and  
230 splitting<sup>37</sup>. Species additions from taxonomic change can constitute a significant proportion of newly described



231 species (e.g., ref. 43, 45), and is expected to increase with advances in molecular technologies<sup>24</sup>. Our  
232 analyses, which focused on the temporal differentiation of known species numbers, are therefore not able to  
233 distinguish between new discoveries and species additions resulting from taxonomic change. Further  
234 interpretation of our results must be conducted with caution. Given that taxonomic change remains a  
235 significant challenge in biogeographical and macroecological research<sup>37</sup>, future efforts should focus on  
236 integrating historical records of taxonomic change at broad taxonomic and spatial scales. This would allow for  
237 a more robust assessment of the influences of incomplete biodiversity knowledge, extending beyond the  
238 incomplete taxonomy to include other challenges such as a lack of species distribution knowledge.

239

## 240 **Conclusion**

241 Our work provides a dynamic perspective on estimated global biodiversity patterns, showing that ongoing  
242 species discoveries substantially alter our understanding of macroecological patterns and relationships. We  
243 found evidence of notable reconfigurations in the relative geography of diversity centers, as well as shifts in  
244 the inferred importance of environmental drivers, particularly for understudied groups such as reptiles and  
245 amphibians in the tropics. These findings indicate that current estimates of global diversity patterns and their  
246 drivers for poorly studied taxonomic groups are less reliable than often assumed, and that relying on them  
247 may compromise conservation planning under climate change. Addressing these challenges requires  
248 renewed taxonomic and survey efforts, especially in tropical and montane regions. We therefore echo  
249 Wilson's<sup>50</sup> call for "more boots on the ground" to accelerate species discoveries and close critical biodiversity  
250 knowledge gaps.

251

## 252 **Materials and Methods**

### 253 **Data compilation**

254 We compiled species range maps from multiple sources for terrestrial vertebrates. For birds, we used data  
255 from the Handbook of the Birds of the World and BirdLife International version 7<sup>51</sup>. For mammals and  
256 amphibians, we used the International Union for Conservation of Nature Red List of Threatened Species<sup>35</sup>.  
257 We sourced reptile species range maps from Roll et al.<sup>5</sup>. We filtered the range polygons for all taxa to include  
258 only extant, native or reintroduced species. Following the guideline of the IUCN mapping standards, we  
259 included species with a presence code of 1-3 (extant, probably extant, possibly extant), an origin code from 1-  
260 2 (native, reintroduced), and a seasonal code from 1-3 (resident, breeding, non-breeding). For reptiles, we  
261 included all available range maps, as they all represent extant and native species. Our dataset comprised  
262 range maps for 10,856 bird, 5,586 mammal, 9,880 reptile, and 7,714 amphibian species.

263

### 264 **Taxonomy**

265 We standardized species nomenclature and taxonomic authorities for all taxa to ensure consistency. For  
266 birds, we followed the taxonomy of the Handbook of the Birds of the World and BirdLife International version  
267 7<sup>51</sup>. For mammals and amphibians, we used the IUCN Red List<sup>35</sup>, supplemented with The Mammal Diversity  
268 Database<sup>24</sup> and Amphibian Species of the World 6.2<sup>52</sup> where IUCN data were incomplete. For reptiles, we first  
269 referenced The Reptile Database<sup>53</sup> checklist (version 2 March 2024). We then resolved any discrepancies by  
270 cross-referencing against The Reptile Database synonym checklist (version April 2023) and synonyms listed  
271 in the IUCN Red List<sup>35</sup>. We conducted additional literature searches to complete taxonomic authority  
272 information for reptile species when necessary.

273

### 274 **Diversity patterns**

275 To analyze global diversity patterns, we first aggregated species range maps onto a global hexagonal grid.  
276 We used the 'dggrid' R package<sup>54</sup> to create grid cells, with each cell covering an area of 7,774 km<sup>2</sup>. The  
277 hexagonal grid can minimize geographic distortions in area and distance, making it suitable for  
278 macroecological studies<sup>55</sup>. We then overlaid the grid with global land cover data, excluding any cells that the  
279 remaining land area was less than half of the original cell size. Within each remaining cell, we determined the  
280 presence and number of species by intersecting with species ranges.

281

282 To explore temporal dynamics of global vertebrate diversity gradients under species discoveries, we  
283 estimated diversity patterns at 10-year intervals beginning in 1920, representing a time span of one century.  
284 We did this by considering the cumulative number of species described and published up to the end of each  
285 time period. The latest description date in our dataset was 2019 for birds, 2020 for mammals and amphibians,  
286 and 2015 for reptiles. For convenience, we hereafter refer to 2020 as the upper time limit for all groups.

287  
288 To account for the potential effects of biogeographic history<sup>38</sup>, we assigned each hexagonal grid cell to one of  
289 six zoogeographic regions: Australian, Neotropical, Nearctic, Palearctic, Ethiopian, and Oriental. This  
290 delineation followed the work of Holt et al.<sup>56</sup> and Ficetola et al.<sup>57</sup>. In total, our final analyses included 9,716  
291 bird, 5,245 mammal, 8,646 reptile, and 7,267 amphibian species.

### 293 **Environmental variables**

294 To identify the environmental relationships for vertebrate diversity, we selected environmental variables that  
295 reflect contemporary climate, environmental heterogeneity, and past climate change. These variables have  
296 been used widely as important predictors of vertebrate diversity<sup>58–61</sup>. We sourced present climatic conditions  
297 from the Climatologies at high resolution for the earth's land surface areas (CHELSA) dataset at a resolution  
298 of 30 arc-sec<sup>62</sup>. We included mean annual temperature (bio1), annual range of temperature (bio7), annual  
299 precipitation (bio12), precipitation seasonality (bio15), and mean monthly precipitation of the warmest quarter  
300 (bio18). We initially considered other variables representing climate harshness, such as temperature  
301 seasonality (bio4), mean daily minimum air temperature of the coldest month (bio6), and mean monthly  
302 precipitation amount of the driest quarter (bio17), but excluded them due to high collinearity with other  
303 selected climatic variables (Pearson's  $r > 0.7$ ). Environmental heterogeneity was represented by elevation  
304 range, calculated as the difference between maximum and minimum altitude from the Global multi-resolution  
305 terrain elevation data 2010 at a resolution of 30 arc-sec<sup>63</sup>. The magnitude of past climate change was  
306 quantified using temperature and precipitation anomalies from Last Glacial Maximum (~21,000 years ago),  
307 measured as the difference between present and LGM conditions derived from CHELSA-TraCE21k<sup>64</sup>.

### 309 **Analyses**

#### 310 **Estimation of diversity metrics**

311 We evaluated vertebrate diversity patterns using two diversity metrics: species richness and range-weighted  
312 rarity<sup>65</sup>. We calculated species richness as the total number of species present in each hexagonal grid cell. To  
313 emphasize the conservation value of narrow-ranging species, we also calculated range-weighted rarity. We

314 derived this metric by summing the rarity value of each species within a given cell, where rarity of a species  
315 was defined as the inverse of the number of cells it occupied. This approach is frequently used to prioritize  
316 conservation efforts for species with restricted ranges<sup>10,30,36</sup>. Considering the inherent L-shaped distribution of  
317 species ranges in our dataset, where a majority of species are narrowly distributed, we adjusted the rarity  
318 calculation to prevent disproportionate influence of highly restricted species. We therefore added a constant  
319 offset to the denominator, that is the number of occupied cells, in the rarity calculation. This constant value  
320 was set as the 75<sup>th</sup> percentile of the overall species ranges for each vertebrate group. This method can  
321 balance the influences of narrowly distributed species, avoiding the creation of too many high-rarity “islands”  
322 while still emphasizing their conservation importance.

323

### 324 **Identifying diversity centers**

325 To evaluate the temporal dynamics of biodiversity centers over the past century, we identified the top 5% and  
326 10% of hexagonal grid cells for both species richness and range-weighted rarity. These cells, which represent  
327 the highest diversity, were considered as diversity centers. These centers were identified for time periods  
328 1920 and 2020 in our analysis. We then tracked the spatial shifts in these centers by comparing their locations  
329 across different time periods.

330

### 331 **Spatial models**

332 To explore the shifts in the relationships between species diversity and environmental variables over time, we  
333 performed linear regressions of species richness against environmental variables. These explanatory  
334 variables included contemporary climate (mean annual temperature, temperature range, annual precipitation,  
335 precipitation seasonality, and precipitation of the warmest quarter), environmental heterogeneity (elevation  
336 range), and past climate change (anomaly in temperature and precipitation since Last Glacial Maximum). We  
337 natural log-transformed species richness, and square root-transformed environmental variables to reduce the  
338 skewness. We then standardized all variables to zero mean and unit standard deviation for comparison  
339 across models.

340

341 Given the detection of significant spatial autocorrelation in our initial linear models, we used simultaneous  
342 autoregressive regressions (SAR) with the error type, implemented with the ‘spatialreg’ R package<sup>66</sup>. To  
343 define the spatial neighbor structure for the SAR models, we used a distance band approach. We determined  
344 the optimal distance by iteratively testing a distance from 100 km to 3000 km in an increment of 200 km. We  
345 selected the best distance that yielded the lowest Akaike information criterion (AIC), highest Nagelkerke’s  
346 pseudo R<sup>2</sup>, and an insignificant Moran’s I test for residual spatial autocorrelation. With the appropriate

347 distance, spatial autocorrelation was significantly accounted for. As biogeographic history might vary among  
348 regions<sup>38</sup>, we repeated the spatial model analysis independently for each biogeographic realm.

349

350 To test for the difference in the effect of environmental factors on species richness between 1920 and 2020,  
351 we utilized a *z*-test. As species richness of these two time periods are from the same locations and violate the  
352 assumption of independence, we incorporated the covariance between the coefficient estimates in our *z*-test.  
353 To correctly estimate the coefficient covariance, we first extracted the residuals from each spatial model.  
354 These residuals were then transformed using the spatial error parameter and a weight matrix. This allowed us  
355 to compute the coefficient covariance. The *z*-test was formulated as follows:

356

$$z = \frac{\beta_1 - \beta_2}{\sqrt{SE(\beta_1)^2 + SE(\beta_2)^2 - 2 \times Cov(\beta_1, \beta_2)}}$$

357 Here,  $\beta_1$  and  $\beta_2$  are the coefficients of the environmental factor from two spatial models,  $SE(\beta)$  represent the  
358 standard error for each coefficient,  $Cov(\beta_1, \beta_2)$  represent the estimated covariance between the two  
359 coefficients. A P value less than 0.05 from the *z*-test indicates a significant difference between the two  
360 coefficients across the two time periods.

361

## 362 Data availability

363 Species range maps are availability from several public repositories: birds from the Handbook of the Birds of  
364 the World and BirdLife International version 7 (<https://datazone.birdlife.org>); mammals and amphibians from  
365 the IUCN Red List of Threatened Species (<https://www.iucnredlist.org/>); and reptiles from ref. 5  
366 (<https://doi.org/10.1038/s41559-017-0332-2>). Taxonomic data are available as follows: birds from the  
367 Handbook of the Birds of the World and BirdLife International version 7 (<https://datazone.birdlife.org>);  
368 mammals from the IUCN Red List of Threatened Species (<https://www.iucnredlist.org/>) and The Mammal  
369 Diversity Database (<https://www.mammaldiversity.org/>); reptiles from The Reptile Database ([https://reptile-  
370 database.org/](https://reptile-database.org/)); amphibians from the IUCN Red List of Threatened Species (<https://www.iucnredlist.org/>) and  
371 Amphibian Species of the World 6.2 (<https://amphibiansoftheworld.amnh.org/>). Environment data are available  
372 at CHELSA (<https://chelsa-climate.org/>) and GMTED2010 (<http://pubs.er.usgs.gov/publication/ofr20111073>).

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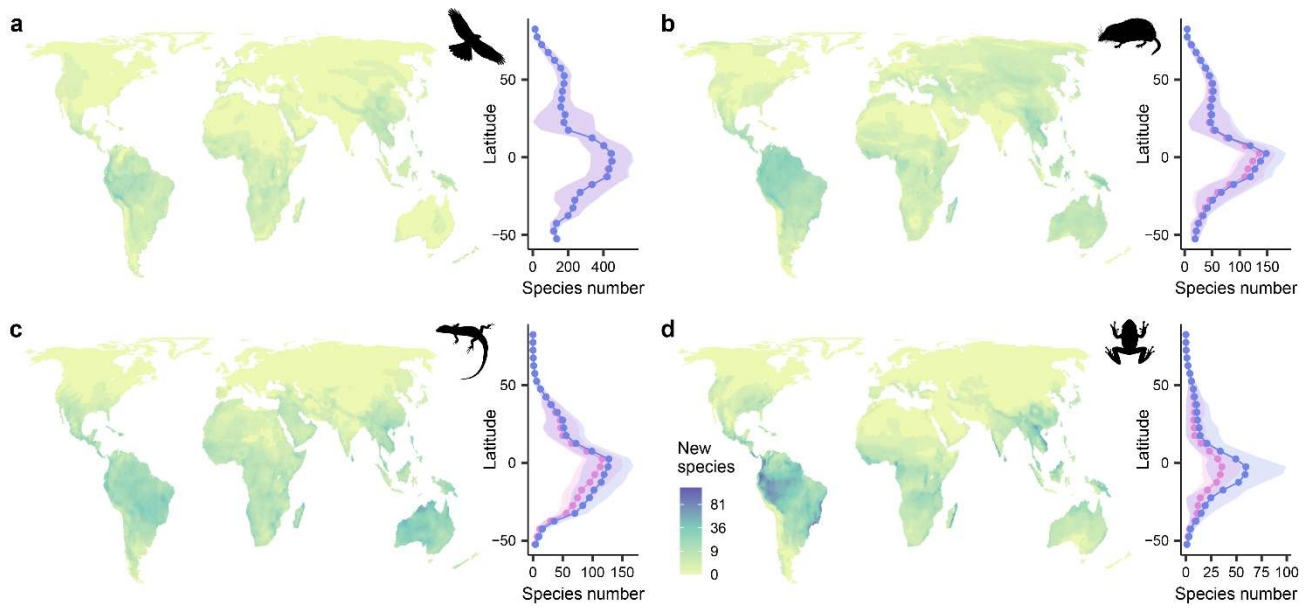
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503 substantial contributions from D.L., J.-C.S., W.-Y.G., W.D., M.Z and J.L. All authors commented on the draft.

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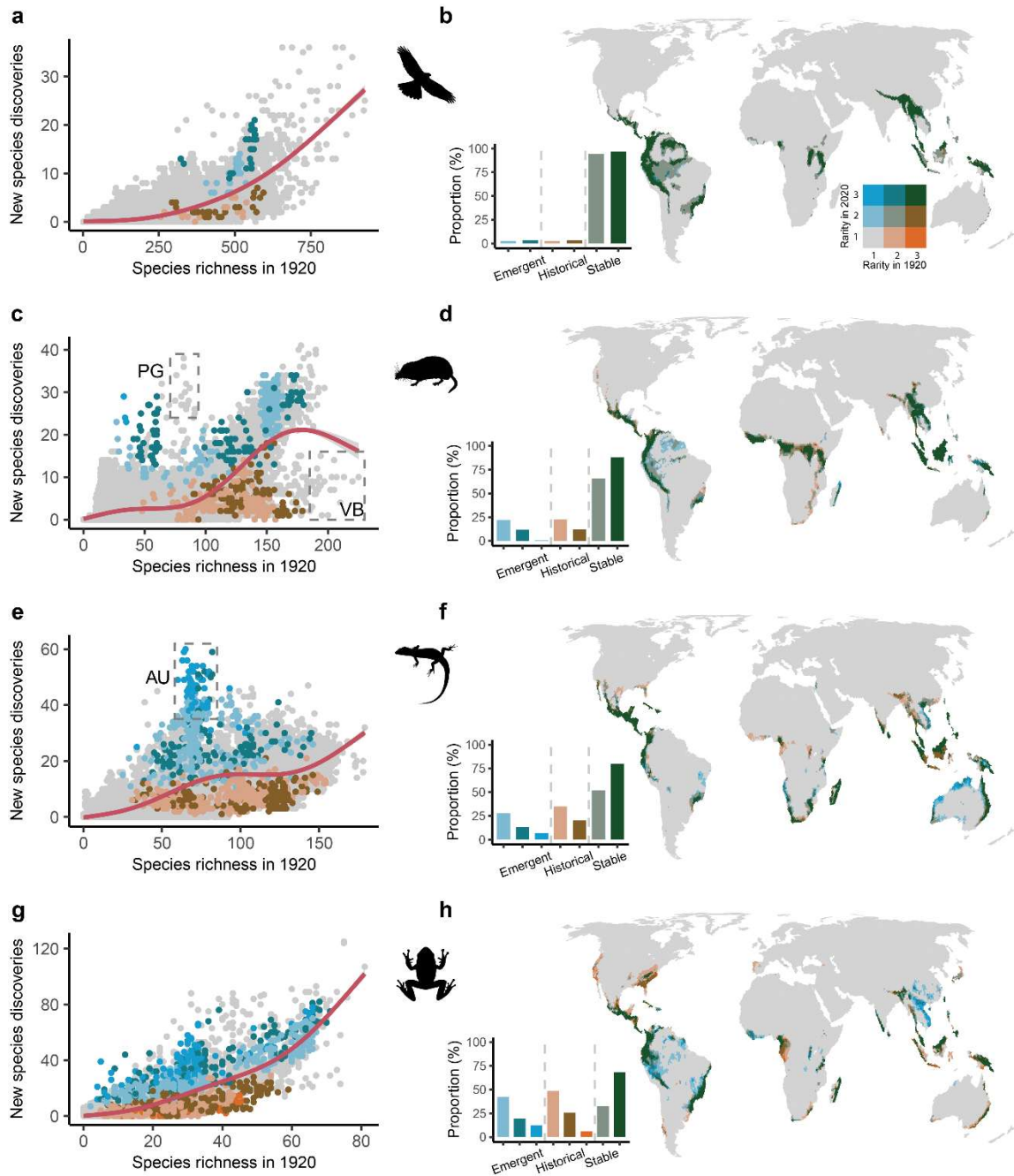




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506 **Fig. 1 New species discoveries in the tropics steepen the latitudinal diversity gradient.** a-d, Maps show  
 507 the diversity of new species discovered between 1920-2020 for birds (a), mammals (b), reptiles (c), and  
 508 amphibians (d). The plots illustrate the corresponding shift in the latitudinal diversity gradient (LDG) for total  
 509 species number in 1920 (red) and 2020 (blue). All maps use an identical color scale. In the plots, solid circles  
 510 represent mean species number per 5-degree latitudinal band, and the shaded area indicates the standard  
 511 deviation (s.d.) around the mean. Silhouettes are from PhyloPic (credits: a, Andy Wilson; b, Leonardo  
 512 Ancillotto; c, Kailah Thorn; d, Vijay Karthick).

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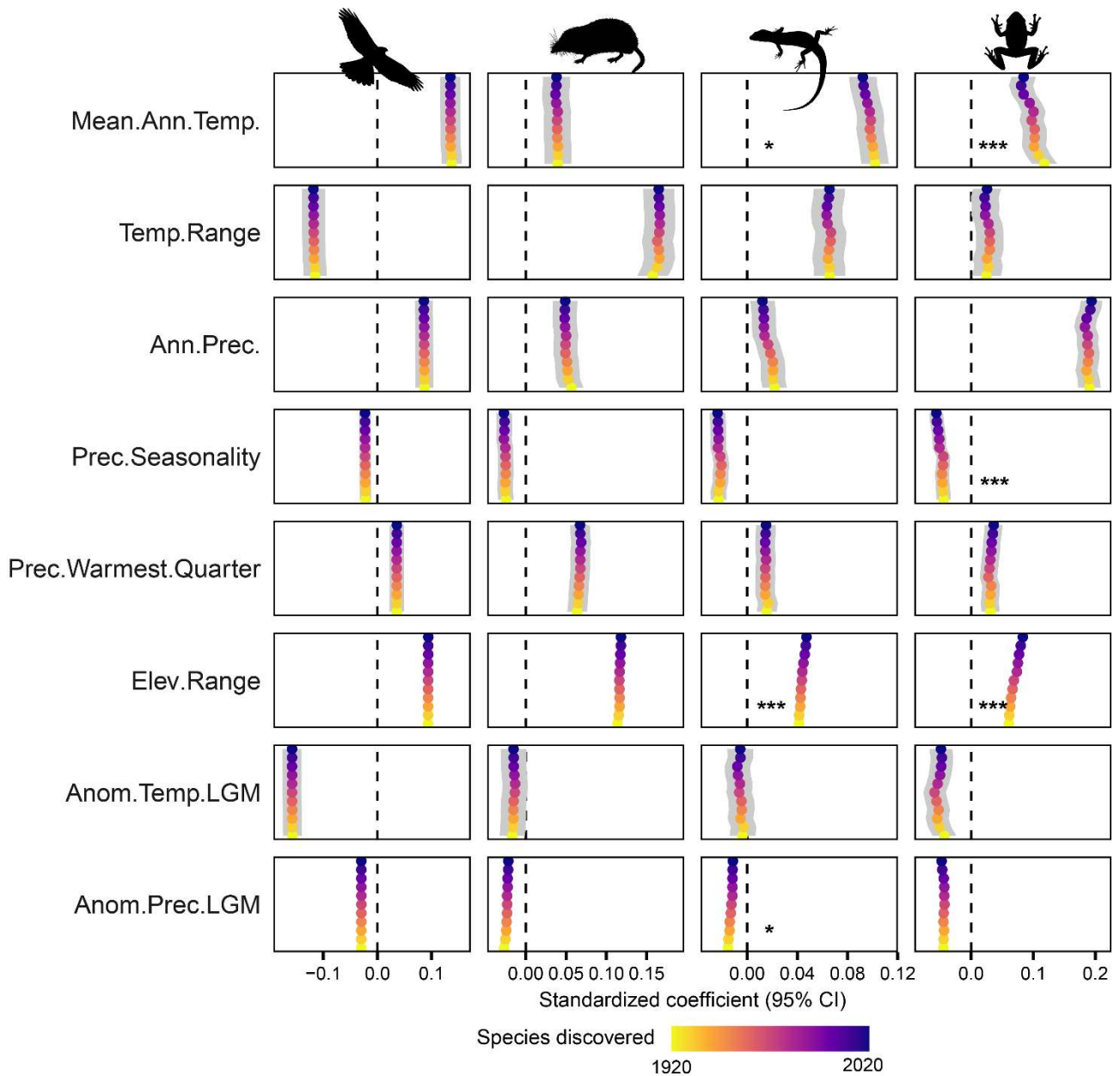
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**Fig. 2 New species discoveries reshaped estimated diversity patterns.** **a, c, e, g,** The relationship between species richness in 1920 and subsequent discoveries (1920-2020) for birds, mammals, reptiles, and amphibians. The solid lines represent a generalized additive model spline. Annotated labels highlight regions: Papua New Guinea (PG); Victoria Basin (VB); Australia (AU). **b, d, f, h,** Maps show the shift in diversity centers of range-weighted rarity between 1920 and 2020. Dark shades indicate regions in the top 5% of rarity, medium shades the top 5-10%, and light shades and grey indicate regions outside the top 10%. Shifted diversity centers are highlighted in color: emergent centers (regions that emerged as diversity centers after new species discoveries, blue), historical centers (regions initially identified as diversity centers but have since diminished, brown), and stable centers (regions that remained stable across discoveries, green). Inset bar plots show the proportion of shifted diversity centers for each group. Silhouettes are from PhyloPic (credits: a, b, Andy Wilson; c, d, Leonardo Ancillotto; e, f, Kailah Thorn; g, h, Vijay Karthick).



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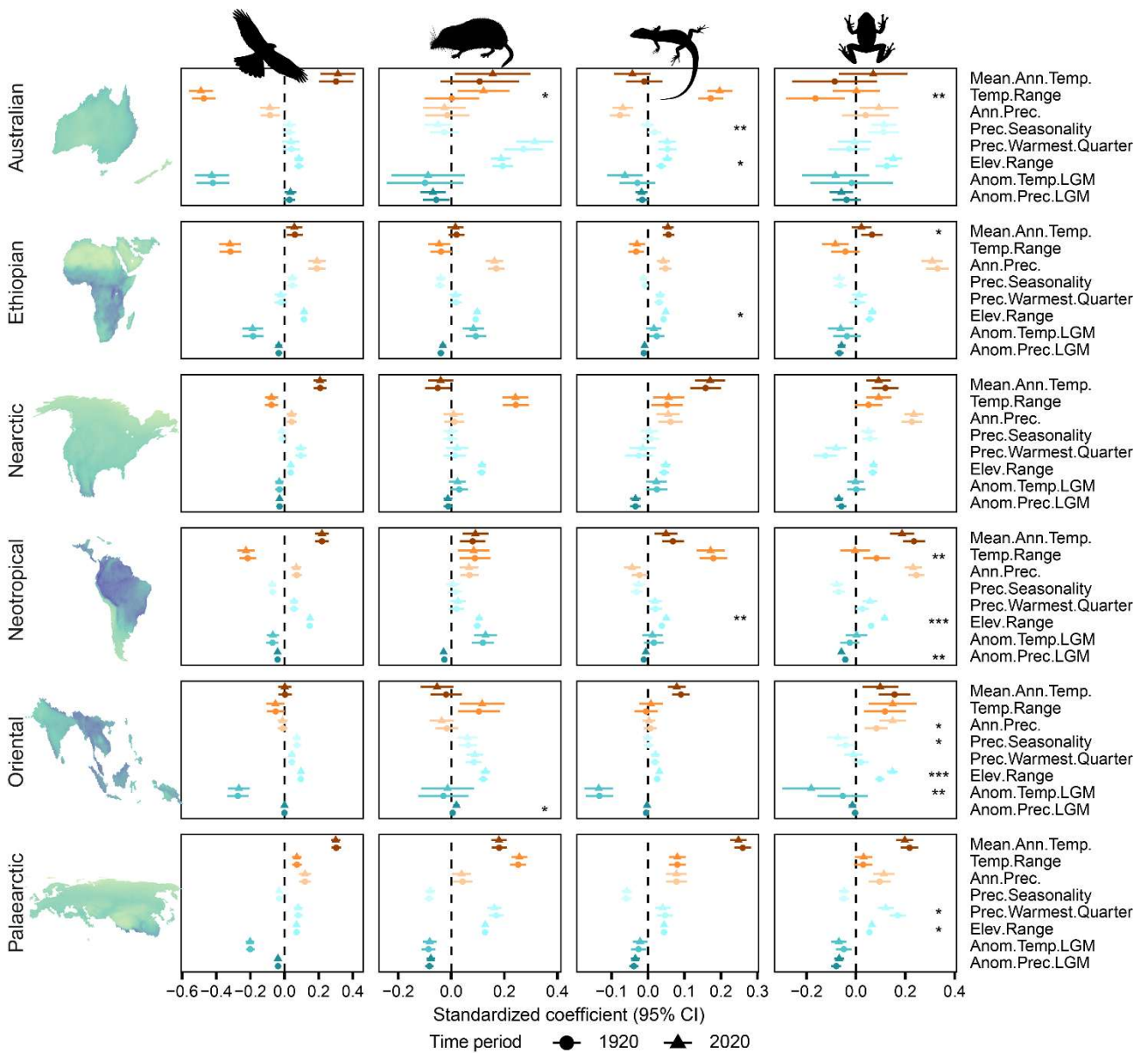
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**Fig. 3 Shifts in estimated relationships between environment and vertebrate diversity at the global**

**scale.** Standardized coefficients from simultaneous autoregressive models illustrate the change in species richness relationships for birds, mammals, reptiles, and amphibians from 1920 to 2020. The shaded grey area represents the 95% confidence interval. Significance was tested using a modified z-test to control for the temporal dependence. Asterisks indicate a significant difference in environmental variable coefficients between 1920 and 2020:  $P < 0.001$  (\*\*\*) , and  $0.01 < P < 0.05$  (\*). Mean.Ann.Temp., mean annual temperature (bio1); Temp.Range, annual range of temperature (bio7); Ann.Prec., annual precipitation (bio12); Prec.Seasonality, precipitation seasonality (bio15); Prec.Warmest.Quarter, mean monthly precipitation of the warmest quarter (bio18); Elev.Range, elevation range; Anom.Temp.LGM, temperature anomaly since Last Glacial Maximum; Anom.Prec.LGM, precipitation anomaly since Last Glacial Maximum. Silhouettes are from PhyloPic (credits: Andy Wilson, bird; Leonardo Ancillotto, mammal; Kailah Thorn, reptile; Vijay Karthick, amphibian).



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542 **Fig. 4 Contrasting environmental driver estimates for vertebrate diversity across biogeographic**  
 543 **realms.** Standardized coefficients from simultaneous autoregressive models represent predictors of species  
 544 richness in 1920 (circles) and 2020 (triangles). Panels show results for birds (left), mammals (middle left),  
 545 reptiles (middle right), and amphibians (right). Error bar indicates 95% confidence intervals. Biogeographic  
 546 realm map is shown in gradient of known vertebrate diversity in 2020. Significance was tested using a  
 547 modified *z*-test to control for the dependence between 1920 and 2020. Asterisks indicate a significant  
 548 difference in environmental variable coefficients between 1920 and 2020:  $P < 0.001$  (\*\*\*),  $0.001 < P < 0.01$  (\*\*),  
 549 and  $0.01 < P < 0.05$  (\*). Mean.Ann.Temp., mean annual temperature (bio1); Temp.Range, annual range of  
 550 temperature (bio7); Ann.Prec., annual precipitation (bio12); Prec.Seasonality, precipitation seasonality  
 551 (bio15); Prec.Warmest.Quarter, mean monthly precipitation of the warmest quarter (bio18); Elev.Range,  
 552 elevation range; Anom.Temp.LGM, temperature anomaly since Last Glacial Maximum; Anom.Prec.LGM,  
 553 precipitation anomaly since Last Glacial Maximum. Silhouettes are from PhyloPic (credits: Andy Wilson, bird;  
 554 Leonardo Ancillotto, mammal; Kailah Thorn, reptile; Vijay Karthick, amphibian).

555

556 **Table 1 Number and proportion of discovered terrestrial vertebrate species between 1920 and 2020.**

557 Proportion of discovered species within each time period is shown in parentheses.

Time period	Birds	Mammals	Reptiles	Amphibians
1920-1940	408 (3.8%)	466 (8.3%)	755 (7.6%)	629 (8.2%)
1940-1960	134 (1.2%)	204 (3.7%)	525 (5.3%)	500 (6.5%)
1960-1980	87 (0.8%)	241 (4.3%)	845 (8.6%)	941 (12.2%)
1980-2000	111 (1%)	357 (6.4%)	1,179 (11.9%)	1,256 (16.3%)
2000-2020	92 (0.8%)	506 (9.1%)	1,708 (17.3%)	2,547 (33%)
<b>1920-2020</b>	<b>832 (7.7%)</b>	<b>1,774 (31.7%)</b>	<b>5,012 (50.7%)</b>	<b>5,873 (76.1%)</b>

558