

# 1 Combining taxonomic, phylogenetic and functional diversity reveals new global 2 priority areas for tetrapod conservation

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## 8 Abstract

9 We are in the midst of a sixth mass extinction but little is known about the global patterns of biodiversity when  
10 accounting for taxonomic, phylogenetic and functional information. Here, we present the first integrated  
11 analysis of global variation in taxonomic, functional diversity and phylogenetic diversity of more than 17,000  
12 tetrapod species (terrestrial mammals, amphibians, reptiles and birds). We used a new metric (z-Diversity)  
13 able to synthesize taxonomic, functional and phylogenetic information across different sets of species to  
14 provide a comprehensive estimation of biodiversity. Our analyses reveal that hotspots of tetrapod diversity are  
15 clustered in specific regions of the world such as central Africa and the Indian peninsula, and that climate  
16 stability and energy availability have an overarching importance in explaining tetrapod spatial patterns. Future  
17 research might take advantage of these methods to perform an informed prioritization of protected areas.  
18

## 19 Introduction

20 Humans drive patterns of biodiversity in the Anthropocene to the point that the world is facing the sixth mass  
21 extinction<sup>1</sup>, where nearly 1 million species are estimated to be threatened with extinction with severe  
22 consequences for ecosystem health and human wellbeing<sup>2,3</sup>. Biodiversity is a multidimensional metric<sup>4</sup> and  
23 species loss does not only entail a reduction in species richness, but potentially affect also the evolutionary  
24 history (phylogenetic diversity – PD<sup>5</sup>) and the functional structure (functional diversity – FD<sup>6</sup>) of natural  
25 communities<sup>7,8</sup>. While PD can provide information on how past dispersal events may have shaped current  
26 species assemblages<sup>9</sup>, FD depicts ecosystem functions and associated services than simple patterns of species  
27 richness and turnover might not completely disclose<sup>10</sup>. Particularly, the regional loss of PD or FD may lead  
28 local assemblages towards the loss of evolutionary history or important functions likely jeopardizing crucial  
29 ecosystem processes, and potentially leading to higher homogenization<sup>11</sup>. In recent years, increased data  
30 availability (e.g. species spatial distribution, functional or genetic data) has improved our understanding of  
31 global diversity patterns across the tree of life<sup>9,12–14</sup>, including the development of conservation targets based  
32 on the assumption that conserving species with unique evolutionary history indirectly preserve also other  
33 diversity facets (e.g. EDGE project<sup>15</sup>). Nevertheless, recent findings seem to suggest that focusing on PD alone  
34 might not ensure the conservation of all facets of diversity<sup>16</sup>, but the strength of the relationship between PD  
35 and FD is still debated in literature<sup>17,18</sup>. Given these premises, the inclusion of different diversity facets beyond  
36 taxonomic diversity is essential for a thorough understanding of the processes shaping life on Earth<sup>19,20</sup>, and  
37 ideally to reevaluate global priority areas for biodiversity conservation<sup>21–24</sup>. Despite the pivotal role of FD and  
38 PD on ecosystem functioning and stability<sup>10,25,26</sup>, little is known about how biodiversity conservation could  
39 benefit from an integration of its different diversity facets<sup>21,27</sup>.

40 Here, we provide the first integrated analysis of global variation in taxonomic, functional diversity and  
41 phylogenetic diversity of extant tetrapods (terrestrial mammals, amphibians, reptiles and birds) by presenting  
42 a new metric (z-Diversity) integrating species richness, PD and FD in a single measure that can be combined  
43 across different groups of species to provide a comprehensive estimation of biodiversity. We focused on  
44 Tetrapods which represent half of the vertebrate species living on our planet and are among the most described  
45 taxa (in terms of spatial distribution, conservation status and functional traits) on our planet. There are

46 continuous evidences of ongoing global decline for all these species<sup>28–32</sup>, to the point that approximately one  
47 third of them are threatened with extinctions, spanning from 14% of birds to 40% of amphibians<sup>33</sup>. Tetrapods  
48 have important ecological roles within natural ecosystems<sup>34,35</sup>, thus preserving higher tetrapod diversity should  
49 buffer the effects of accelerated global change<sup>36,37</sup>, promoting ecosystem stability<sup>38</sup>.  
50 Many studies tried to disentangle tetrapod spatial patterns mainly focusing on mammals and birds<sup>21,35,39,40</sup>, but  
51 see<sup>19,41</sup>), and their taxonomic patterns<sup>42–44</sup>, whereas little attention have been paid to the spatial patterns of the  
52 other diversity facets (i.e. PD and FD)<sup>9,39,40</sup>. Several hypotheses (reviewed in Fine<sup>45</sup>) have been postulated to  
53 explain broad-scale patterns of species diversity, usually relying solely on species richness, with a lack of  
54 general consensus so far. These relate diversity to the variation in water-energy dynamics<sup>46,47</sup> or link it with  
55 macroevolutionary aspects<sup>48</sup>, historical factors<sup>44</sup> and species coexistence<sup>49</sup>. Nevertheless, there are no well-  
56 established mechanistic hypotheses about the drivers of broad-scale patterns of PD and FD, and if they might  
57 respond to different factors with respect to the one described for species richness. Given these premises, an  
58 integrated metric such as z-Diversity might help to identify global priority areas whose protection would  
59 maximize tetrapod diversity. In addition, testing the relationship between z-Diversity and some variables  
60 related to past climate change, biogeography history, energy availability and land use legacies might shed light  
61 on their relative influence in shaping global tetrapod spatial patterns. Our analyses reveal that hotspots of  
62 tetrapod diversity are clustered in specific regions of the world such as central Africa and Indian peninsula.  
63 Finally, climate stability and energy availability revealed to be the best predictors in explaining the spatial  
64 variation across all tetrapod groups.  
65

## 66 **Results**

### 67 **Spatial mismatch between diversity facets**

68 For our analysis, we collated a large database of 17,341 tetrapod species encompassing 3,912 terrestrial  
69 mammals 3,239 amphibians, 3,338 reptiles and 6,852 birds for which accurate range estimates were available  
70 based on International Union of Conservation of Nature (IUCN) data<sup>50</sup> which were subsequently converted to  
71 hexagonal equal-area grid cells (cell resolution 23,322 km<sup>2</sup>) on which we compiled the species list in each cell  
72 for each taxonomic group. Later, we selected a set of functional traits characterizing tetrapod species from  
73 public databases<sup>51,52</sup> along with their phylogenies<sup>20,40,53,54</sup>. Due to the presence of missing values among traits,  
74 for each group we performed a phylogenetically informed trait imputation procedure followed by a sensitivity  
75 analysis to evaluate imputation performance following Carmona et al.<sup>8</sup>, both using phylogenetic information  
76 that functional traits only. Briefly, for each taxonomic group we first compute the functional space using  
77 principal component analysis (PCA); we then artificially removed trait values in a reduced set of species which  
78 were later imputed with the complete database. The ability in retrieving species position in the functional space  
79 was used as an indicator of the performance of the imputation process. Our simulations showed that the  
80 imputation procedure performed quite well in retrieving the positions of species in the functional space for all  
81 groups, but using phylogenetic information halves the errors on average with respect to the imputation realized  
82 with traits information only (Supplementary Figure 1, see methods for more details).

83 For each grid cell and for each group, we therefore estimated species richness (SR), Faith's PD<sup>5</sup> and FD which  
84 was expressed as functional richness (FRic). Since both PD and FRic depend on species richness<sup>55</sup>, we  
85 performed null model simulations to obtain standardized effect sizes – SES computed as follows: [SES =  
86 (Metric<sub>obs</sub> – mean(Metric<sub>null</sub>))/SD<sub>null</sub>]. SES indicate the degree of deviation of a given metric (expressed in SD  
87 units) with respect to simulated values. The three diversity metrics thus obtained (SR, sesPD, sesFRic) were  
88 later scaled and centered to unit variance (zSR, zPD, zFRic) and averaged into a single indicator of diversity  
89 (z-Diversity). The arithmetic mean among the z-Diversities of the four taxonomic groups provided a new  
90 overall metric able to synthesize the total diversity (taxonomic, functional and phylogenetic aspects) contained  
91 in a set of species.

92 Overall, we observed congruent spatial pattern in species richness and sesPD for all taxonomic groups. In  
93 contrast, sesFRic showed some striking differences especially between mammals and reptiles (see for instance  
94 central Africa and Indian peninsula in Supplementary Figure 2, where to a higher sesFRic was associated a  
95 lower sesPD). Moreover, negative correlations between species richness and sesPD were detected across all  
96 taxonomic groups while there was a slight positive correlation between sesPD and sesFRic (Supplementary  
97 Table 1). Tetrapod z-Diversity is strongly correlated with zFRic (Pearson's correlation  $r = 0.76$ ,  $p < 0.001$ ;  
98 all correlations were spatially corrected) and to a lesser extent to zSR ( $r = 0.34$ ,  $p < 0.01$ ) whereas a not  
99 significant correlation was detected with zPD ( $r = 0.17$ ,  $p > 0.05$ ). z-Diversity was also strongly correlated

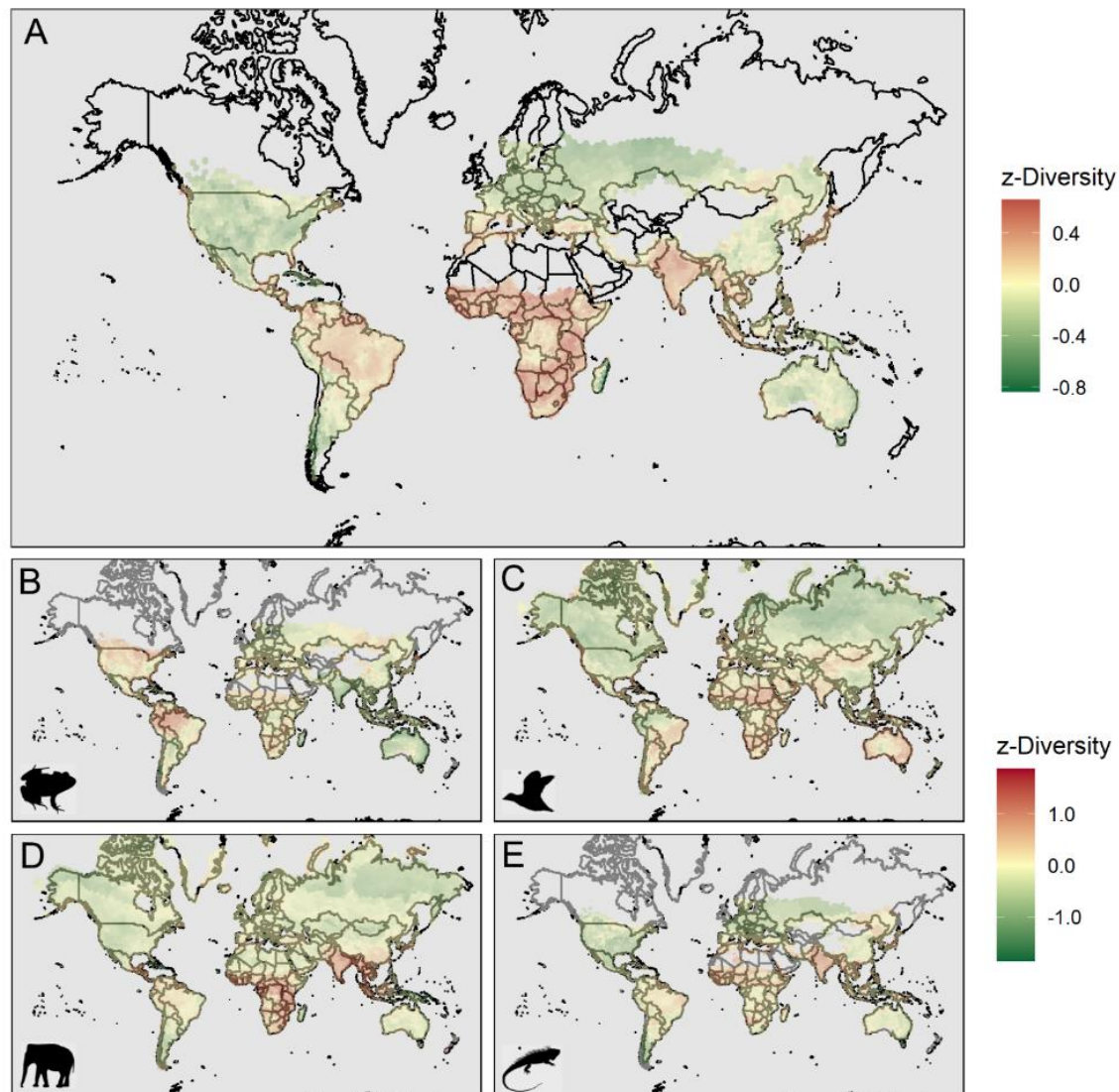
100 with zFRic across all groups; additionally for mammals and birds we observed also a significant correlation  
101 with zSR and zPD, respectively (Supplementary Table 2). Notably, Afrotropics and Indomalayan realms  
102 showed an overall even dispersion on both sesPD and sesFric with respect the other realms, in contrast  
103 Neotropic realm was mainly driven by both phylogenetic and functional clustering across all groups  
104 (Supplementary Figure 3).

105

### 106 **Global priority areas**

107 Global tetrapod z-Diversity is highest in Africa and South-East Asia followed by Central and South America,  
108 Japan and the Mediterranean basin (Figure 1A). Looking at the single groups (Figures 1B,C,D,E), mammals  
109 z-Diversity was higher in Africa and Indian peninsula, whereas amphibians showed a higher z-Diversity  
110 especially in the Amazon basin. Reptiles displayed the highest variation in Africa and South-East Asia while  
111 bird assemblages showed higher z-Diversity in southern hemisphere with peaks especially in Africa and  
112 Oceania. Interestingly, hotspots of tetrapod z-Diversity (the richest 5% of grid cells) were largely clustered in  
113 African continent with few spots in Indian peninsula and South America (tropical Andes, northeastern coast,  
114 Figure 2A). These patterns were mirrored by all the considered groups (Figure 2B,C,D,E), except for  
115 amphibians whose higher z-Diversity resulted to be largely clustered in South America.

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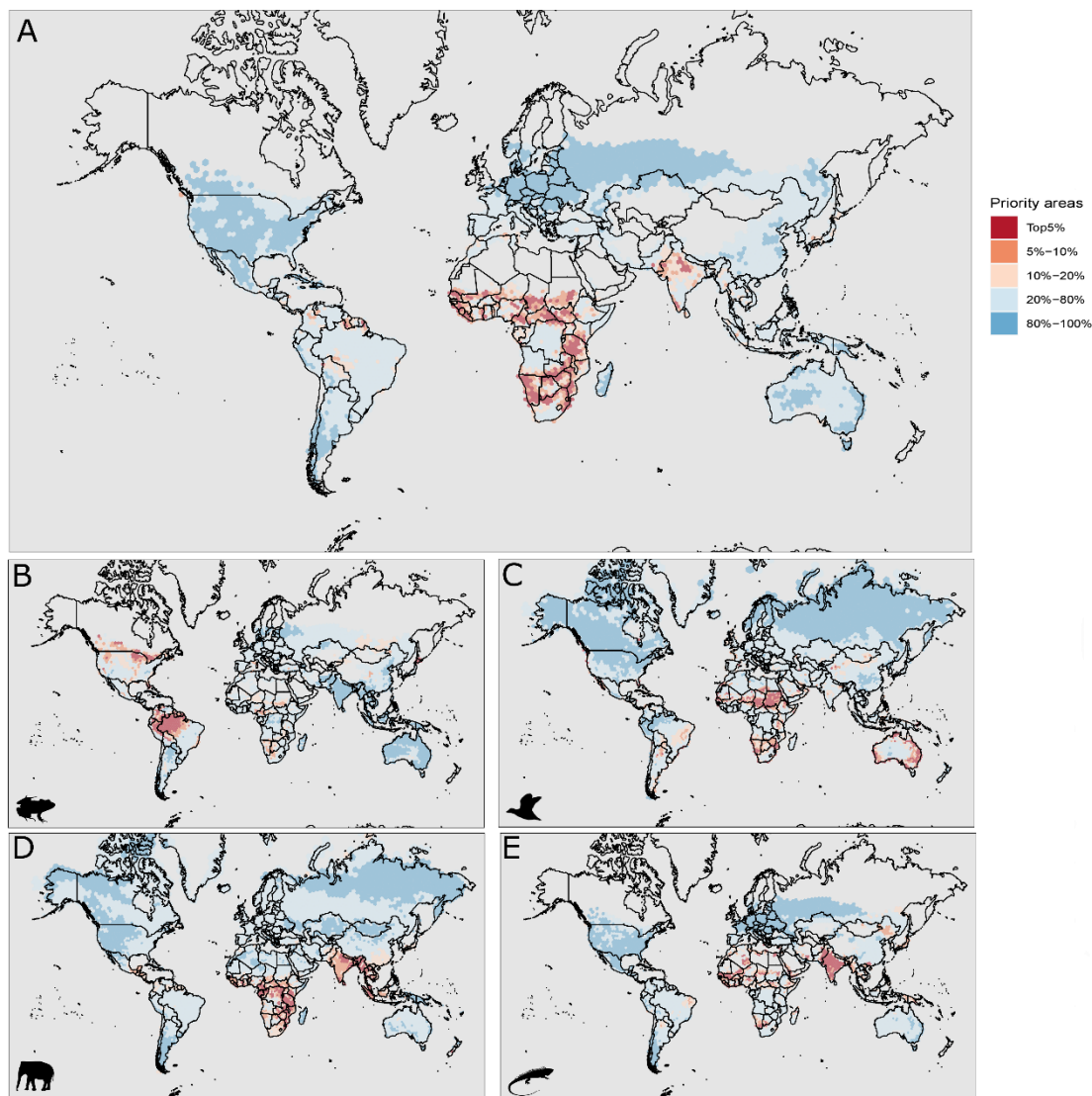
118 **Figure 1.** Global patterns of z-Diversity expressed averaging z-scores of single diversity facets in each  
119 taxonomic groups (zSR, zPD, zFRich). These were later mediated across groups to obtain tetrapod diversity.  
120 (A) Tetrapoda, (B) Amphibia, (C) Aves, (D) Mammalia, (E) Reptilia. Silhouettes were retrieved from PhyloPic  
121 ([www.phylopic.org](http://www.phylopic.org)).

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123

124 **Climate stability and energy availability shapes tetrapod diversity**

125 The global patterns of tetrapod z-Diversity were highly predictable by the set of variables that we chose ( $R^2$   
126  $=0.85\pm 0.04$ , Root Mean Square Error -RMSE  $=0.24\pm 0.06$ ; average  $\pm$  SD). Our model showed that the global  
127 pattern of z-Diversity was mainly driven by energy availability and climate variation since Late Quaternary,  
128 rather than by current or past anthropogenic factors (Figure 3, Table 1). Within taxonomic groups  
129 (Supplementary Figures 4-7), results were relatively concordant, only amphibians departed from this general  
130 pattern, probably due to their higher dependency on water. In addition, whereas the diversity of mammals,  
131 birds and reptiles increased along with evapotranspiration, the diversity of amphibians showed a negative  
132 relationship with PET (Figure 3). In contrast, birds were primarily driven by a positive relation with PET,  
133 while all other variables showed a comparable influence in the model. In terms of model performance, RMSE  
134 within individual groups was higher than those of the tetrapod model ( $\approx 0.41$ ) coupled with a small reduction  
135 in  $R^2$  ( $\approx 0.78$ ).



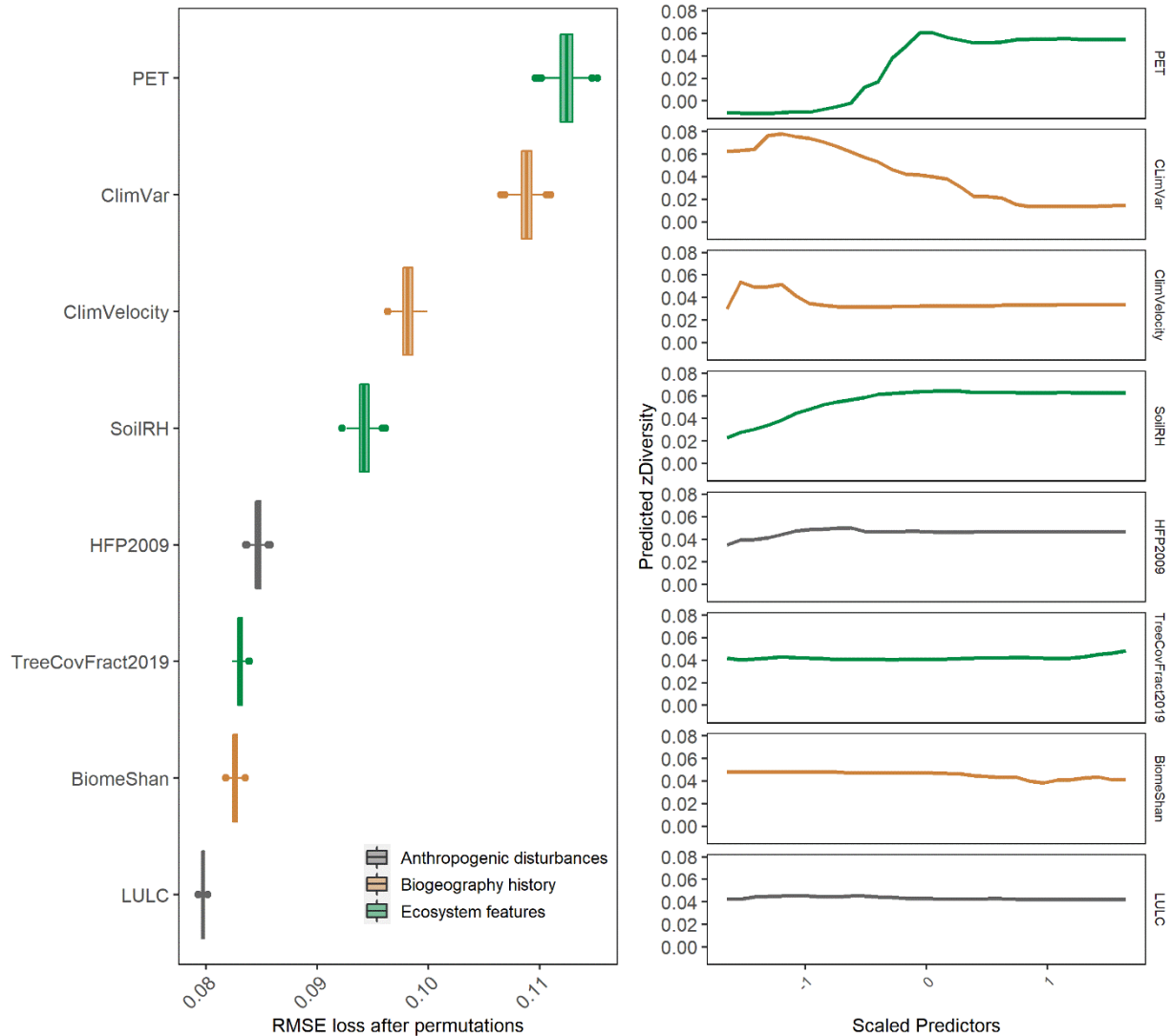
136 **Figure 2.** Global hotspots of z-Diversity. Darkest tones denote 10% of the richest grid cells while darker tones  
137 5% and 2.5%, respectively. (A) Tetrapoda, (B) Amphibia, (C) Aves, (D) Mammalia, (E) Reptilia. Silhouettes  
138 were retrieved from PhyloPic ([www.phylopic.org](http://www.phylopic.org)).  
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140 **Discussion**

141 We collated, for the first time at a global scale, the taxonomic, phylogenetic and functional characteristics of  
142 all groups of terrestrial vertebrates and summarized it in a single index. Accounting for all the three diversity  
143 facets across different taxonomic groups revealed conservation priority areas that are usually overlooked in  
144 global conservation schemes that use less comprehensive information<sup>41</sup>. These new hotspots of diversity

145 include arid and semi-arid environments, especially in the Mediterranean basin, central Asia, southern coast  
146 of Australia or in South America (e.g. Brazilian caatinga). Interestingly, despite the relatively lower number  
147 of tetrapod species with respect to Neotropics, the Afrotropical and Indomalayan realms stand out as hotspots  
148 of a high diversity (Supplementary Figure 3). This result is in agreement with previous studies on individual  
149 taxonomic groups (e.g. amphibians<sup>20</sup>, mammals<sup>39,56</sup>, reptiles<sup>41</sup>), but here we present the first comprehensive  
150 assessment showing this trend across all terrestrial vertebrates and considering multiple facets of diversity.  
151 Interestingly, the pattern of z-Diversity is primarily driven by functional diversity, as suggested by the high  
152 correlation between z-Diversity and zFRic ( $r = 0.76$ ), highlighting the importance to consider functional  
153 information to provide reliable evaluation of species diversity patterns. Afrotropics showed the highest values  
154 of sesFRic with respect to random expectations especially for mammals and reptiles (Supplementary Figure  
155 3). This pattern might be explained by the high intrinsic megafaunal diversity reported for this continent<sup>56,57</sup>.  
156 African continent was probably the first one which experienced some moderate megafaunal loss (e.g.  
157 carnivores and proboscidean) already in Early Pleistocene (~ 1 Ma) likely due to the appearance of *Homo*  
158 *erectus*<sup>58</sup>, which were later somehow dampened thanks to coevolution with *Homo sapiens*. In contrast, outside  
159 *H. sapiens* area of origin, subsequent extinction waves occurred coinciding more or less with the expansion of  
160 humans across the globe<sup>59</sup>. In addition to this, the Great American Biotic Interchange (GABI) – the interchange  
161 between North and South American faunas associated with the formation of the Isthmus of Panama – seemed  
162 to have enhanced the extinction and the consequent reduction of diversity in South American mammals<sup>60</sup>.  
163 We detected also dominant phylogenetic clustering suggesting that environmental filtering and inter-clade  
164 competitions have shaped local assemblages<sup>61</sup>. Indeed, clades with rapid speciation rates such as primates in  
165 Africa and ovenbirds (Furnariidae) in Central-South America or closely related species tended to co-occur  
166 more frequently at smaller scales, as a results of local processes of radiation and dispersal limitations<sup>62</sup>.  
167 Nonetheless, multiple processes can interact together in defining local assemblages in space and time, and  
168 more studies linking mechanistically trait evolution and biogeographic history can help in this sense (e.g.  
169 process-based models<sup>63</sup>). Moreover, the relatively low correlation between sesPD and sesFRich implies a  
170 spatial mismatch in the global spatial diversity patterns, suggesting also that phylogenetic diversity captures  
171 only a portion of functional diversity in agreement with recent works<sup>16,64</sup>.  
172 Energy availability and climate stability confirmed to have an overarching importance to explain tetrapod  
173 diversity. Water–energy dynamics are important in describing species richness patterns for plants<sup>65</sup> and  
174 animals<sup>46,66</sup>, but their relationship with the other diversity facets has been poorly investigated at a global scale  
175 (but see<sup>67</sup>). Generally, higher energy (i.e., higher PET) is linked to a higher resource availability which in turn  
176 promotes greater species packing (i.e., more species coexist with narrower niches<sup>68</sup>) and larger population sizes  
177 which may lessen extinction rates<sup>47</sup>. When considered individually, only amphibians departed from this general  
178 pattern, due to their higher dependency on water. The high importance of soil humidity in amphibians  
179 (Supplementary Figure 5) is not surprising since it helps in keeping balanced their hydric state<sup>69</sup>. Also the  
180 negative relation with PET compared to the positive of all other groups could be explained by the property of  
181 this metric, which tends to increase towards dry environments, not reflecting water balance as accurately as  
182 Actual Evapotranspiration (AET)<sup>70</sup>. Model outputs also indicated that climate stability promotes higher  
183 diversity, probably through the combination of lower extinction rates and high levels of speciation<sup>71,72</sup>,  
184 occurring also at a larger spatial scale. There are compelling evidences of higher extinction rates towards the  
185 poles for different taxonomic groups<sup>67,73</sup> further corroborating the idea that climate stability and evolutionary  
186 processes influence species richness latitudinal gradient<sup>42</sup> through region-specific accumulation of diversity<sup>74</sup>,  
187 which is consistent with the CSH. Accordingly, species inhabiting more stable regions tend to display restricted  
188 thermal preferences and higher specialization<sup>48,75,76</sup>, thanks also to the higher frequency of speciation events<sup>77</sup>  
189 driven by the intimate link between temperature and ecological and evolutionary rates<sup>78</sup>. In contrast, extinctions  
190 might be higher in climatic unstable regions<sup>79</sup>, being triggered by variations in Earth's orbit causing recurrent  
191 climatic shifts across the globe<sup>80</sup>. For instance, higher extinction rates occurred during cold periods, especially  
192 for those taxonomic groups with poor dispersal abilities<sup>81</sup> (e.g. reptiles). To the best of our knowledge, this is  
193 the first evidence demonstrating how climate stability influences broad-scale patterns of species diversity,  
194 considering all three diversity facets. Lastly, we found no consistent effect of past and recent Land Use Land  
195 Changes similarly to what observed for genetic diversity<sup>12</sup>, even though future projections of land-use changes  
196 seem to strongly affect Earth's biodiversity<sup>82,83</sup>. Another explanation for this lack of signal might rely in the  
197 relatively coarse scale used in this study along with the lack of finer spatio-temporal data able to depict these  
198 patterns. Even though some taxa (e.g. small-ranged species) or regions (e.g. tropics) might have some spatial  
199 biases<sup>84</sup>, and despite the potential lack of inclusion of important evolutionary or ecological variables (e.g.

200 speciation and dispersal rate), our models indicated that the selected variables are able to describe most of the  
 201 global variation in tetrapod diversity.  
 202 Our novel approach allows to consider all components of biodiversity and average them across taxonomic  
 203 groups. Future research can take advantage of these methods to perform an informed prioritization of protected  
 204 areas<sup>23,24</sup>, which could enhance the achievement of Aichi Biodiversity targets, whose progress for some  
 205 indicators are still not satisfactory<sup>2</sup>. More importantly, the cells hosting a higher tetrapod diversity are often  
 206 located in regions under high human pressure (e.g. Southeast Asia, Mediterranean coast)<sup>19,85</sup> enhancing the  
 207 need for a transnational cooperation, especially in the countries with lower GDP in order to preserve also the  
 208 “option-value” of natural ecosystems.



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**Figure 3.** Variable importance ranked by the RMSE loss after permutations (left panel) and marginal effects  
 213 of the different predictors (right panel) of the random forest model using tetrapod z-Diversity as response  
 214 variable. *ClimVar* and *ClimVel* represented the average rate of change during the time-series (expressed in  
 215 °C/century and m/yr, respectively) since Last Glacial Maximum. *BiomeShan* described the variation in biome  
 216 patterns over the last 140 ka expressed using the Shannon index. *SoilRH*, *PET*, and *TreeCovFract2019*  
 217 represented soil humidity, Potential Evapotranspiration and forest cover updated to 2019, respectively. *LULC*  
 218 expresses the fraction of grid cell under anthropogenic land use since 8000 BC, while *HFP2009* is the 2009  
 219 Human Footprint index.  
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**Table 1.** Model output showing the variable importance expressed using Root Mean Square Error (RMSE) loss (average  $\pm$  SD) for each variable considering all tetrapod pooled and each taxonomic group independently. *ClimVar* and *ClimVel* represented the average rate of change during the time-series (expressed in  $^{\circ}\text{C}/\text{century}$  and  $\text{m}/\text{yr}$ , respectively) since Last Glacial Maximum. *BiomeShan* described the variation in biome patterns over the last 140 ka expressed using the Shannon index. *SoilRH*, *PET*, and *TreeCovFract2019* represented soil humidity, Potential Evapotranspiration and forest cover updated to 2019, respectively. *LULC* expresses the fraction of grid cell under anthropogenic land use since 8000 BC, while *HFP2009* is the 2009 Human Footprint index. RMSE and  $R^2$  were obtained using spatial cross-validation. *N* represents the number of grid cells used to train the models. Please note z-Diversity was computed only in the cells where all the three metrics (zSR, zPD, zFD) were available.

Predictor	Tetrapoda	Mammalia	Amphibia	Reptilia	Aves
PET	0.112 $\pm$ 0.0009	0.056 $\pm$ 0.0011	0.211 $\pm$ 0.0014	0.237 $\pm$ 0.0019	0.349 $\pm$ 0.0026
ClimVar	0.109 $\pm$ 0.0007	0.058 $\pm$ 0.0009	0.174 $\pm$ 0.0009	0.186 $\pm$ 0.0010	0.198 $\pm$ 0.0011
ClimVelocity	0.098 $\pm$ 0.0007	0.003 $\pm$ 0.0010	0.155 $\pm$ 0.0007	0.215 $\pm$ 0.0019	0.184 $\pm$ 0.0005
SoilRH	0.094 $\pm$ 0.0006	0.051 $\pm$ 0.0011	0.182 $\pm$ 0.0011	0.162 $\pm$ 0.0004	0.188 $\pm$ 0.0007
HFP2009	0.085 $\pm$ 0.0003	0.038 $\pm$ 0.0008	0.177 $\pm$ 0.0012	0.158 $\pm$ 0.0003	0.186 $\pm$ 0.0007
TreeCovFract2019	0.083 $\pm$ 0.0003	0.046 $\pm$ 0.0012	0.168 $\pm$ 0.0011	0.160 $\pm$ 0.0004	0.198 $\pm$ 0.0009
BiomeShan	0.080 $\pm$ 0.0003	0.030 $\pm$ 0.0009	0.143 $\pm$ 0.0005	0.163 $\pm$ 0.0005	0.173 $\pm$ 0.0003
LULC	0.080 $\pm$ 0.0001	0.033 $\pm$ 0.0008	0.146 $\pm$ 0.0006	0.161 $\pm$ 0.0005	0.171 $\pm$ 0.0003
<b>R<sup>2</sup></b>	0.85 $\pm$ 0.04	0.77 $\pm$ 0.04	0.78 $\pm$ 0.05	0.78 $\pm$ 0.04	0.77 $\pm$ 0.03
<b>RMSE</b>	0.24 $\pm$ 0.06	0.44 $\pm$ 0.11	0.45 $\pm$ 0.06	0.40 $\pm$ 0.09	0.37 $\pm$ 0.05
<b>N</b>	4274	6408	4581	4584	6439

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## 235 Methods

236 **Species spatial distribution and environmental data.** We obtained expert-verified range maps of 23,848  
237 tetrapod species from the International Union for Conservation of Nature (IUCN)<sup>50</sup>. Even though these maps  
238 might underestimate the complete extent of occurrence of the species, especially in poorly surveyed regions  
239<sup>84</sup>, these currently represent the best information available. We then excluded marine mammals and range maps  
240 were converted to hexagonal equal-area grid cells with a cell area of 23,322 km<sup>2</sup> using the ‘dggridR’<sup>86</sup> R  
241 package. We chose this resolution because it is close to the finest resolution justifiable for using global data  
242 without incurring in false presences<sup>87</sup>. Species names were standardized using Global Biodiversity Information  
243 Facility (GBIF) Backbone Taxonomy<sup>88</sup> using the R package ‘taxize’<sup>89</sup>.

244 For each grid cell, we computed several environmental predictors depicting spatiotemporal effects of past  
245 climate change/biogeography history, current ecosystem features, and anthropogenic disturbances.  
246 Specifically, we gathered the following environmental data: climate stability since Last Glacial Maximum (ca.  
247 20 kya) was retrieved using two complementary indices reflecting the median rate of change during the time-  
248 series expressed in  $^{\circ}\text{C}/\text{century}$  (*climate variation*<sup>90</sup>, *ClimVar*) and  $\text{m}/\text{yr}$  (*climate velocity*<sup>43</sup>, *ClimVel*). *Biome*  
249 *variation* (*BiomeShan*)<sup>91</sup>, expressed using the Shannon index, described the variation in biome patterns over  
250 the last 140 ka. Gridded databases of *Soil humidity* (*SoilRH*) and *Potential Evapotranspiration* (*PET*) were  
251 obtained from TerraClimate<sup>92</sup>, while forest cover (*TreeCovFract2019*) updated to 2019 was retrieved from  
252 Copernicus Global Land Cover products<sup>93</sup>. Land cover land use (*LULC*) legacy effects were assessed by means  
253 of the data of Kaplan et al.<sup>94</sup>, which reported the fraction of grid cell under anthropogenic land use since 8000  
254 BC, while the 2009 Human Footprint index (*HFP2009*)<sup>95</sup> was used to depict the spatial distribution of the  
255 current human pressure across the globe. *HFP2009* reports for each grid cell a measure of the intensity of eight  
256 metrics of human pressure (i.e., human population density, roads, railways, navigable waterways, built  
257 environments, crop land, pasture land, night-time lights), weighted based on the relative human pressure on  
258 that cell<sup>95</sup>.

259 **Functional traits.** Functional trait data for the different groups were collected using public databases from  
260 different sources. See<sup>8</sup> for a detailed description of the traits used in this study.

261 *Mammals, reptiles and birds.* Data were retrieved from Amniote database<sup>51</sup>, which include traits for 4953  
262 species of mammals, 6567 species of reptiles, and 9802 species of birds. Specifically, this database contains  
263 information of 29 life history traits, of which we selected a subset of traits with information available for at  
264 least 1000 species (see Table S1 in Carmona et al.<sup>8</sup> for more details about traits and their completeness in each  
265 group). For mammals, eight traits were chosen: longevity (long, years), number of litters per year (ly), adult  
266 body mass (bm, g), litter size (ls, number of offspring), weaning length (wea, days), gestation length (gest,  
267 days), time to reach female maturity (fmat, days), and snout–vent length (svl, cm). For birds, we selected the  
268 following traits: number of clutches per year, adult body mass (bm, g), incubation time (gest, days), clutch size  
269 (ls, number of eggs), longevity (long, years), egg mass (em, g), snout-vent length (svl, cm), and fledging age  
270 (fa, days). Regarding reptiles, six traits were selected: number of clutches per year, longevity (long, years),  
271 adult body mass (bm, g), clutch size (ls, number of eggs), incubation time (inc, days), and snout-vent length  
272 (svl, cm).

273 *Amphibians.* Functional trait data of amphibians were retrieved from AmphiBIO database<sup>52</sup>. We selected four  
274 traits that mirror similar information as the one collected for the other three groups (i.e. traits related to body  
275 size, pace of life and reproductive strategies): age at maturity (am, years), body size (bs; measured in Anura as  
276 snout-vent length – SVL – and in Gymnophiona and Caudata as total length in mm); maximum litter size (ls,  
277 number of individuals); and offspring size (os, mm).

278 *Phylogenies.* Phylogenies for each group were downloaded from published papers<sup>20,40,53,54</sup>. Species absent  
279 from the phylogeny were manually added to the root of their genus using the R package ‘phytools’<sup>96</sup>. Since for  
280 mammals and birds multiple phylogenetic trees were available, for these groups we computed a maximum  
281 clade credibility tree (MCC) using the ‘phangorn’<sup>97</sup> R package. To assess the reliability of the information  
282 contained in the MCC, we performed a simulation where we correlated PD obtained from this MCC with  
283 those obtained with 100 phylogenies randomly selected from the original posterior distribution. This test  
284 proved that using the MCC tree is unlikely to affect the computation of PD (Supplementary Figure 8).

285 *Trait imputation and sensitivity analysis.* Since there were gaps in the functional trait data, we imputed  
286 missing traits for each group using ‘missForest’<sup>98</sup> R package. This procedure relied on random forest algorithm  
287 to impute trait data taking advantages also of the phylogenetic relationships among species following the  
288 procedure described in Penone et al.<sup>99</sup>. To further validate this procedure, we performed a sensitive analysis  
289 similarly to the one performed in ref.<sup>8</sup>, but repeating the imputation process using both phylogenetic  
290 information and without it... Our simulations showed that the imputation procedure performed quite well in  
291 retrieving the positions of species in the functional space for all groups, but using phylogenetic information  
292 halves the errors on average with respect to the imputation realized with traits information only (Supplementary  
293 Figure 1)

294 *Calculation of diversity metrics.* Extinct species and species totally lacking evolutionary, functional trait or  
295 spatial data were removed from the database, thus leaving 17,341 species for subsequent analysis ( $N = 3,912$   
296 for mammals,  $N = 3,239$  for amphibians,  $N = 3,338$  for reptiles and  $N = 6,852$  for birds; see Supplementary  
297 Table 3). To map global patterns of tetrapod diversity, we first computed diversity metrics for each taxonomic  
298 group independently. Species richness was estimated as the number of species in each cell; PD represented the  
299 sum of branch length between the root node and tips for the subtree comprising all species in the grid cell, and  
300 was computed using the ‘caper’<sup>100</sup> R package. FD was estimated as described in ref<sup>8</sup>, we first have built a two-  
301 dimensional functional space based on a Principal Component Analysis on the log-transformed and scaled trait  
302 values, then by means of TPD framework<sup>101</sup> and ‘TPD’ and ‘ks’ R packages<sup>102,103</sup>, we estimated cell-based  
303 functional richness (FRic, i.e. the amount of the functional space occupied by an assemblage<sup>101</sup>). Since both  
304 PD and FRic are strongly dependent on species richness, we performed null model simulations to break this  
305 relationship<sup>55</sup> and to compute standardized effect sizes (SES) as  $SES = (\text{Metric}_{\text{obs}} - \text{mean}(\text{Metric}_{\text{null}})) / SD_{\text{null}}$ . To  
306 obtain the null distribution, we randomized 1000 times the community composition of each cell preserving  
307 marginal totals by using the quasiswap algorithm in the R package ‘vegan’<sup>104</sup>. After having computed the SES,  
308 we centered and scaled to unit variance the three diversity indices (i.e., species richness, sesPD, sesFric) for  
309 each group in order to obtain comparable range of variation and then we averaged them to calculate within-  
310 group z-Diversity only for the cells where all the three metrics were available. Finally, tetrapod z-Diversity  
311 was obtained as the arithmetic mean of within-group z-Diversity for each cell where all within-group z-  
312 Diversity values were available. We further computed the Pearson's correlation ( $r$ ) among all diversity facets  
313 by taking into account their spatial structure since all these metrics were measured on the same cells.  
314 Specifically, we used a modified t-test of spatial association<sup>105</sup> implemented in the SpatialPack<sup>106</sup> R package  
315 to test the spatial association between z-Diversity and the three diversity metrics underlying it (zSR, zPD,  
316 zFRic) as well as the correlation among their original values (species richness, sesPD, sesFRic).



317 **Drivers of diversity.** Random forest (RF) is a machine learning algorithm consisting of an ensemble of  
318 classification or regression trees<sup>107</sup>. RF are well suited for modeling large-scale patterns, since they can deal  
319 with large amounts of data, prevent overfitting and multicollinearity, and perform well in presence of complex  
320 interactions or non-linear relationships<sup>108</sup>. RF are effectively used in different research fields such as climate  
321 modelling<sup>109</sup>, species conservation<sup>110</sup> and landscape genetics<sup>111</sup>, among others. We build 5 models using z-  
322 Diversity as a function of environmental variables (one for tetrapod plus one for each individual taxonomic  
323 group) using the framework provided in the ‘ml3’<sup>112</sup> and ‘mlr3spatiotempcv’<sup>113</sup> R packages. We started  
324 building trees using the following parametrization: *ntree* = 500, *mtry* = 1, *min.node.size* = 1, *sample.fraction* =  
325 0.6, which were later tuned using the ‘paradox’<sup>114</sup> R package. Variable importance was determined by  
326 measuring the mean change in a loss function (i.e., Root Mean Square Error - RMSE) after variable  
327 permutations (*N* = 500) using ‘DALEX’ R package<sup>115</sup>. This method assumes that if a variable is relevant for a  
328 given model, we expect a worsening in model’s performance after randomly permuting its values (see<sup>116</sup> for  
329 more technical details). In other words, this method assesses variable importance as the loss in explanatory ability  
330 of the model when that variable is randomized. We also displayed marginal effects of different predictors by  
331 using partial dependence plots computed with the ‘iml’<sup>117</sup> R package.  
332 **Spatial cross validation.** Failing to account for spatial autocorrelation processes in ecology might lead to  
333 biased conclusions<sup>118,119</sup> or to an overoptimistic evaluation of model predictive power<sup>120,121</sup>. For this reason,  
334 we performed an internal spatial cross-validation (spCV) splitting the data into training (70%) and validation  
335 set (30%). We created five spatially disjointed subsets (i.e., partitions) where we introduced a spatial distance  
336 between training and validation set so that these sets are more distant than they would be using random  
337 partitioning<sup>122</sup>. To perform the spCV, we used a nested resampling approach as described in ref.<sup>123</sup>, where outer  
338 resampling evaluated model performance while inner resampling performed tuning of model hyperparameters  
339 for each outer training set. Because nested resampling is computationally expensive, we selected 5 folds with  
340 5 repetitions each to reduce the variance introduced by partitioning in outer resampling and 5 folds in inner  
341 resampling coupled with 50 evaluations of model settings.  
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## 612 **Author contributions**

613 E.T. and C.P.C. co-led and designed the study. E.T., A.T. and C.P.C. extracted and prepared the data, E.T.  
614 performed the statistical analyses. M.P. and D.N.B. contributed to the interpretation of results. E.T. led the  
615 writing of the manuscript with inputs from all the co-authors. All authors approved the submitted version.

616

## Supplementary Information

### Combining taxonomic, phylogenetic and functional diversity reveals new global priority areas for tetrapod conservation

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Supplementary Figure 2: Global patterns of species richness, sesPD and sesFRic across taxonomic groups.

Supplementary Figure 3: Boxplots showing the distribution of species richness, sesPD and sesFRic in each realm

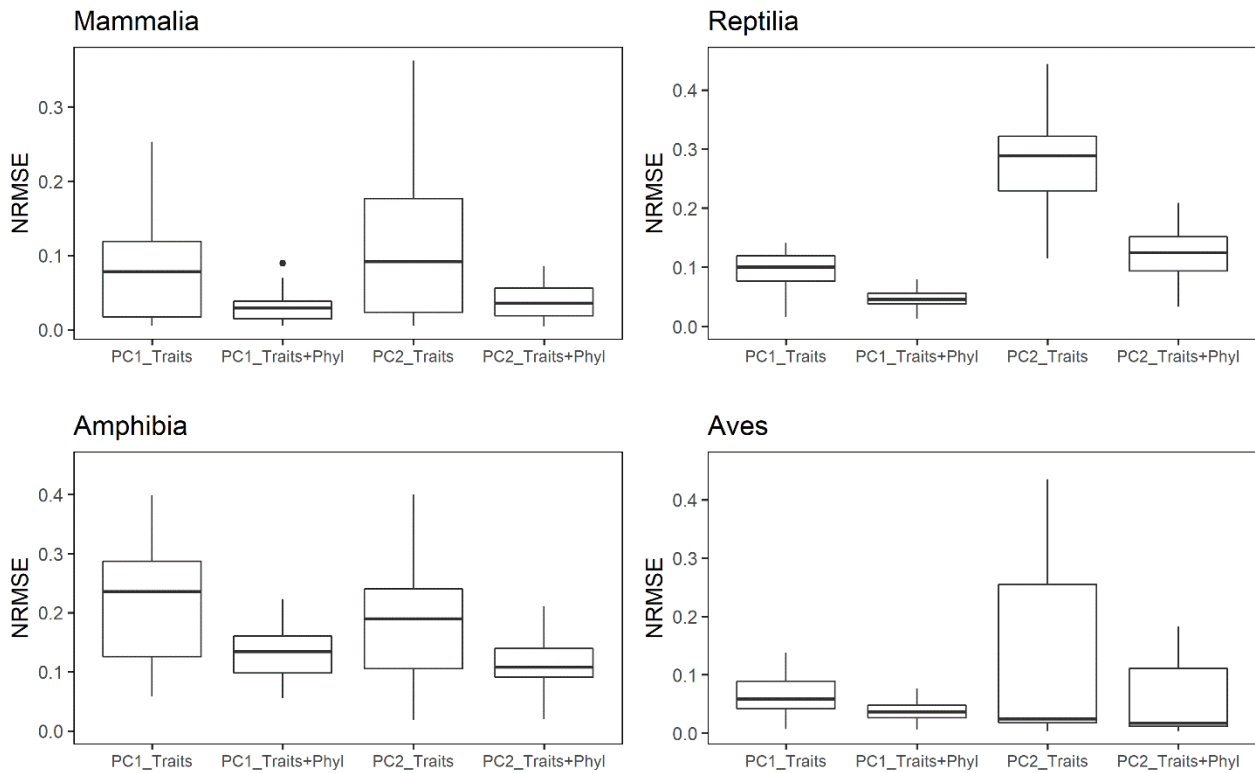
Supplementary Figures 4-7: Variable importance derived from random forest models using zDiversity of single taxonomic groups (Mammals, Amphibians, Reptiles and Birds) as response variable.

Supplementary Figure 8: Comparison of phylogenetic diversity (values calculated with a maximum clade credibility (PD<sub>MCC</sub>) tree and PD calculated with 100 trees randomly selected from the posterior distribution of mammal and bird phylogeny (PD<sub>sim</sub>).

Supplementary Table 1. Pearson's correlation between raw diversity metrics (species richness, sesPD and sesFRic) in each taxonomic groups.

Supplementary Table 2. Pearson's correlation between zDiversity in each taxonomic group and the related standardized diversities.

Supplementary Table 3: Median diversity metric scores for each taxonomic group and for all tetrapod.



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653 **Supplementary Figure 1.** Sensitivity analysis on trait imputation procedure for each taxonomic  
654 group. We simulated missing traits (100 repetitions) starting for a subset of species with complete  
655 trait data. We then randomly selected 10% of species assigning them the structure of missing values  
656 of a random species from the subset of species with missing trait values. Then we combined the three  
657 datasets (90% species with complete traits, 10% with simulated NA and the remaining species with  
658 non-complete trait information). Here we performed two imputation processes: one based solely on  
659 the variance-covariance structure of functional traits and another based on the phylogenetic  
660 information as described in the methods in the main text. For each dataset obtained, we then computed  
661 a functional space using a PCA on which we predicted the position of all species. For only the species  
662 with artificial NA, we evaluated the normalized root mean square error (NRMSE) between the  
663 original position in the functional space and the position calculated after trait imputation, expressed  
664 as the relative range of trait values in the corresponding PC axis.

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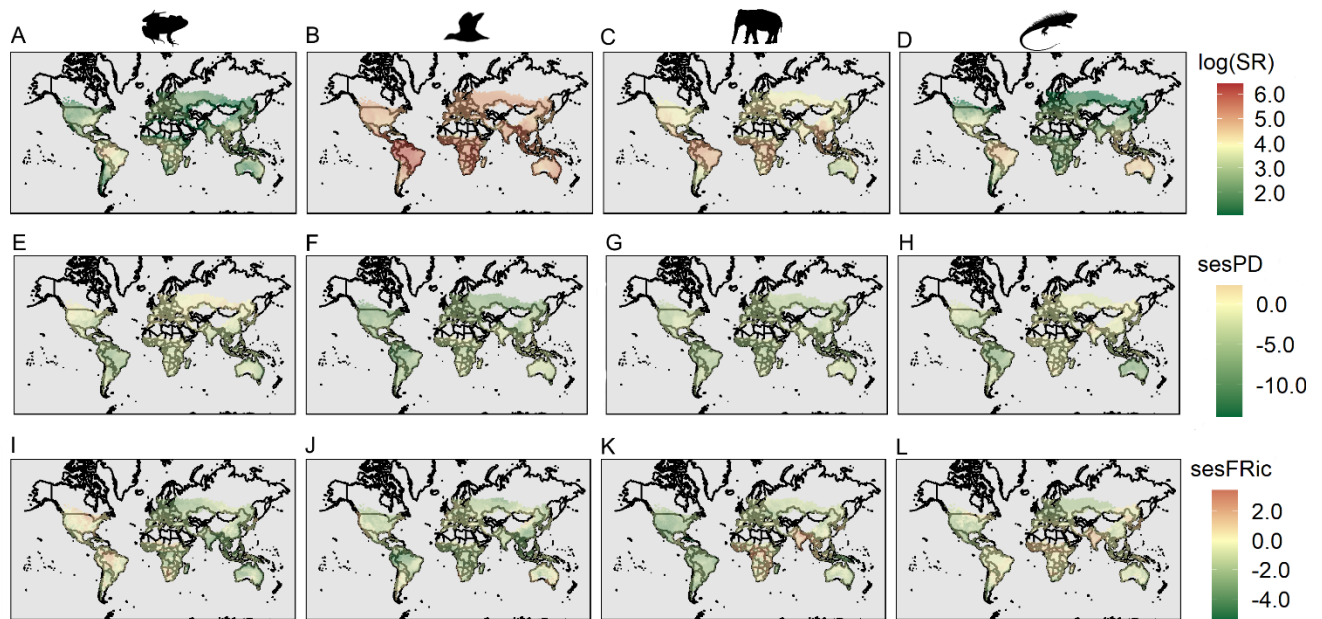
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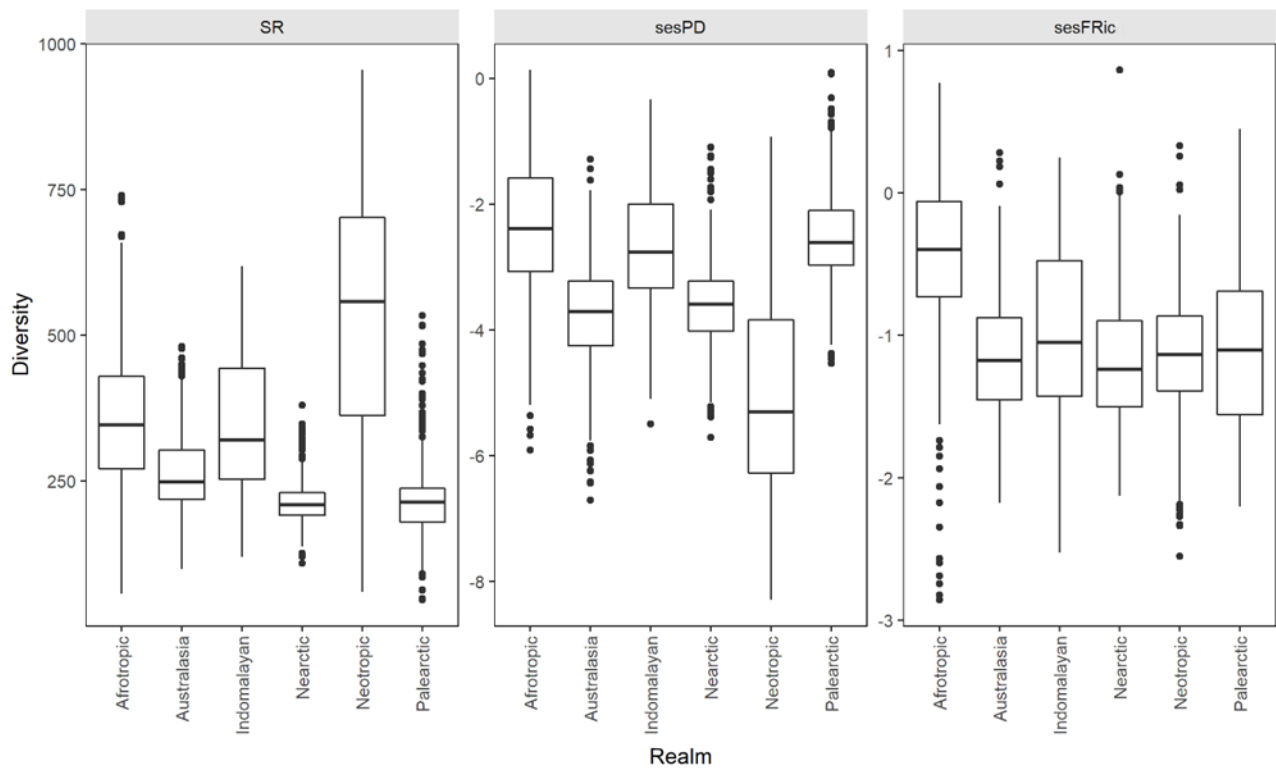
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679 **Supplementary Figure 2.** Global Patterns of species richness (upper panels), sesPD (central panels)  
680 and sesFRic (lower panels). A-E-I) Amphibians, B-F-J) Birds, C-G-K) Mammals, D-H-L) Reptiles.  
681 Please note that species richness is expressed on logarithmic scale and the color scale is centered on  
682 the median value.

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685 **Supplementary Figure 3.** Boxplots showing the distributions of species richness, sesPD and sesFRic  
686 for each realm. Please note that sesPD and sesFRic represents standardized effect sizes of the original  
687 metric.

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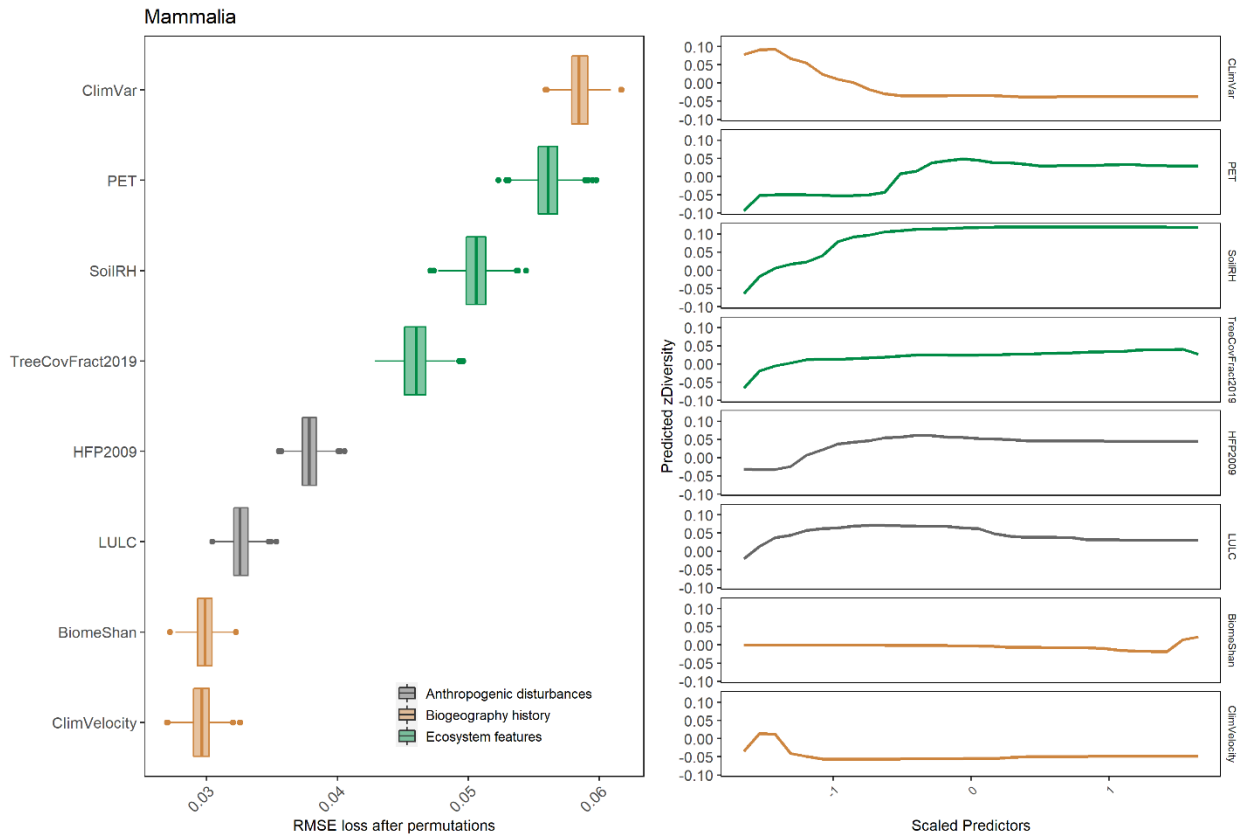
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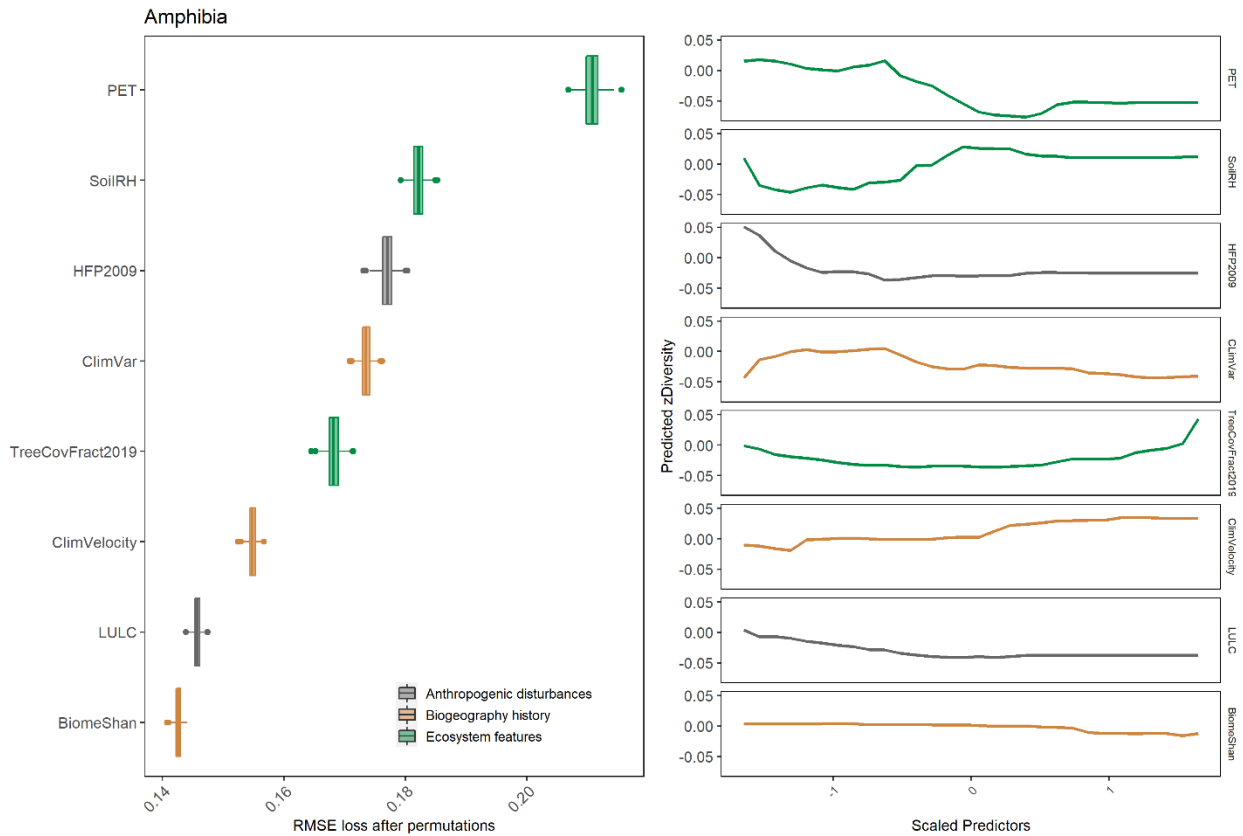
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706 **Supplementary Figure 4.** Variable importance ranked by the RMSE loss after permutations (left  
707 panel) and marginal effects of the different predictors (right panel) of the random forest model using  
708 mammal zDiversity as response variable. *ClimVar* and *ClimVel* represented the average rate of  
709 change during the time-series (expressed in °C/century and m/yr, respectively) since Last Glacial  
710 Maximum. *BiomeShan* described the variation in biome patterns over the last 140 ka expressed using  
711 the Shannon index. *SoilRH*, *PET*, and *TreeCovFract2019* represented soil humidity, Potential  
712 Evapotranspiration and forest cover updated to 2019, respectively. *LULC* expresses the fraction of  
713 grid cell under anthropogenic land use since 8000 BC, while *HFP2009* is the 2009 Human Footprint  
714 index.

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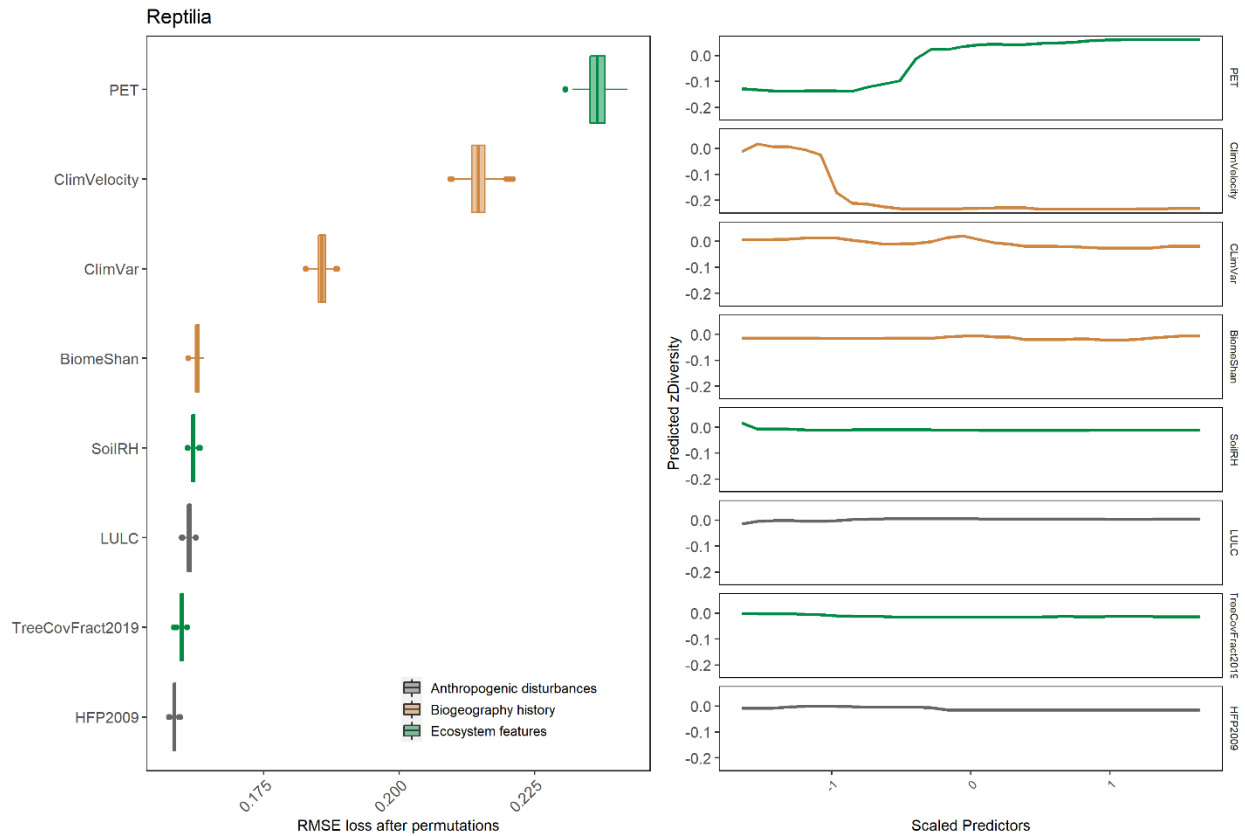


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718 **Supplementary Figure 5.** Variable importance ranked by the RMSE loss after permutations (left  
 719 panel) and marginal effects of the different predictors (right panel) of the random forest model using  
 720 amphibians zDiversity as response variable. *ClimVar* and *ClimVel* represented the average rate of  
 721 change during the time-series (expressed in °C/century and m/yr, respectively) since Last Glacial  
 722 Maximum. *BiomeShan* described the variation in biome patterns over the last 140 ka expressed using  
 723 the Shannon index. *SoilRH*, *PET*, and *TreeCovFract2019* represented soil humidity, Potential  
 724 Evapotranspiration and forest cover updated to 2019, respectively. *LULC* expresses the fraction of  
 725 grid cell under anthropogenic land use since 8000 BC, while *HFP2009* is the 2009 Human Footprint  
 726 index.

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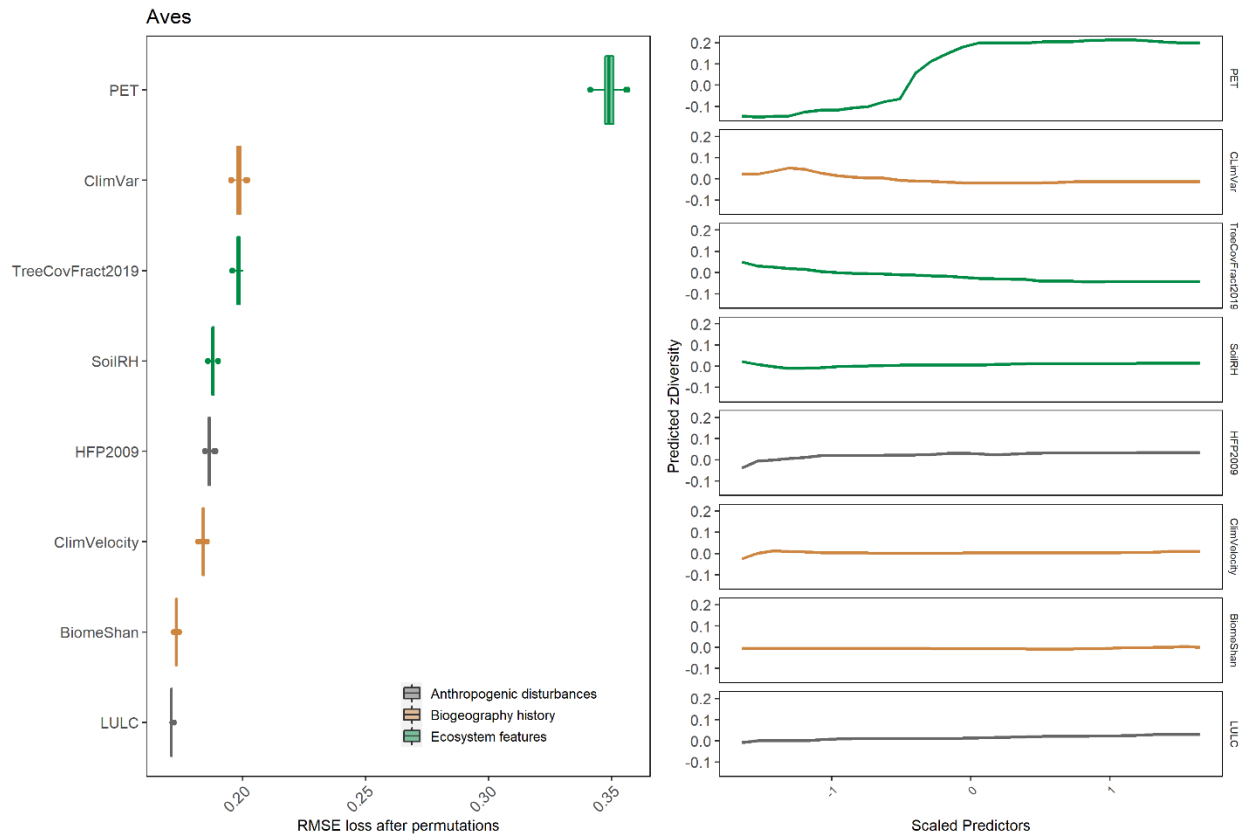


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730 **Supplementary Figure 6.** Variable importance ranked by the RMSE loss after permutations (left  
 731 panel) and marginal effects of the different predictors (right panel) of the random forest model using  
 732 reptilian zDiversity as response variable. *ClimVar* and *ClimVel* represented the average rate of change  
 733 during the time-series (expressed in °C/century and m/yr, respectively) since Last Glacial Maximum.  
 734 *BiomeShan* described the variation in biome patterns over the last 140 ka expressed using the Shannon  
 735 index. *SoilRH*, *PET*, and *TreeCovFract2019* represented soil humidity, Potential Evapotranspiration  
 736 and forest cover updated to 2019, respectively. *LULC* expresses the fraction of grid cell under  
 737 anthropogenic land use since 8000 BC, while *HFP2009* is the 2009 Human Footprint index.

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741 **Supplementary Figure 7.** Variable importance ranked by the RMSE loss after permutations (left  
 742 panel) and marginal effects of the different predictors (right panel) of the random forest model using  
 743 avian zDiversity as response variable. *ClimVar* and *ClimVel* represented the average rate of change  
 744 during the time-series (expressed in °C/century and m/yr, respectively) since Last Glacial Maximum.  
 745 *BiomeShan* described the variation in biome patterns over the last 140 ka expressed using the Shannon  
 746 index. *SoilRH*, *PET*, and *TreeCovFract2019* represented soil humidity, Potential Evapotranspiration  
 747 and forest cover updated to 2019, respectively. *LULC* express the fraction of grid cell under  
 748 anthropogenic land use since 8000 BC, while *HFP2009* is the 2009 Human Footprint index.

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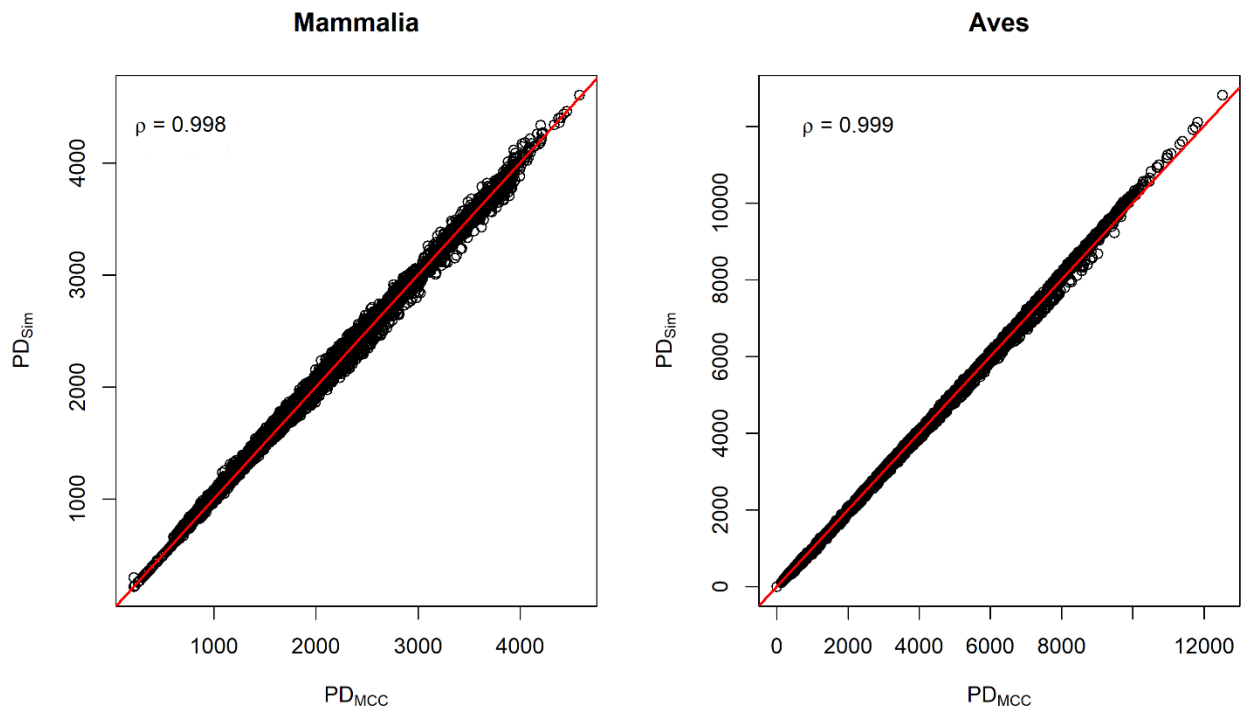
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761 **Supplementary Figure 8.** Comparison of phylogenetic diversity values calculated with a maximum  
762 clade credibility (PD<sub>MCC</sub>) tree and PD calculated averaging the values from 100 trees selected from  
763 the posterior distribution of mammals and birds phylogenies (PD<sub>sim</sub>), red line represents the perfect  
764 fit. In both groups, PD values across assemblages were very similar regardless of the method used  
765 (Spearman's  $\rho > 0.99$ ). We conclude that using a MCC tree should not affect our results.

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781 **Supplementary Table 1.** Pearson's correlations between diversity metrics in each taxonomic groups.  
 782 All the correlations were spatially corrected.

Taxon	SR	sesPD	sesFRic	
Mammalia	-			SR
	-0.70***	-		sesPD
	0.10	0.18	-	sesFRic
Amphibia	-			SR
	-0.78***	-		sesPD
	0.11	0.09	-	sesFRic
Reptilia	-			SR
	-0.87**	-		sesPD
	-0.15	0.32	-	sesFRic
Aves	-			SR
	-0.34	-		sesPD
	-0.53***	0.31*	-	sesFRic

\*\*\* =  $P < 0.001$ ; \*\* =  $P < 0.01$ ; \* =  $P < 0.05$

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784 **Supplementary Table 2.** Pearson's correlation between zDiversity of each taxonomic group and for  
 785 all tetrapod and the related diversity metrics obtained after centering and scaling to unit variance  
 786 species richness (zSR), sesPD (zPD) and sesFRic (zFRic). Please note that overall zDiversity was  
 787 calculated as the arithmetic mean among zSR, zPD and zFRic. All the correlations were spatially  
 788 corrected.

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Taxon	zSR	zPD	zFRic
Mammalia	0.55**	-0.03	0.85***
Amphibia	0.28	0.19	0.89***
Reptilia	0.00	0.34	0.92***
Aves	0.09	0.71***	0.58***
Tetrapoda	0.34**	0.17	0.76***

\*\*\* =  $P < 0.001$ ; \*\* =  $P < 0.01$

790 **Supplementary Table 3.** Median diversity metric scores for each taxonomic group and for all  
 791 tetrapod and the relative coverage in terms of number of species. SR, PD and FRic represent the  
 792 median value of species richness, phylogenetic diversity and functional diversity (expressed as  
 793 functional richness), respectively. of the cells. Please note that for mammals and birds PD was derived  
 794 using a Maximum Credibility Tree.

Clade	Species with functional, phylogenetic and range data	Total species (% total species included in this study)	SR	PD	FRic
Mammalia	3,912	~5,692 (69%)	46	1,623	54
Amphibia	3,239	7,776 (42%)	9	1,109	22
Reptilia	3,338	10,845 (31%)	13	1,134	42
Aves	6,852	10,970 (62%)	133	3,989	72
<b>Tetrapoda</b>	<b>17,341</b>	<b>35,283 (49%)</b>	<b>50</b>	<b>1,964</b>	<b>48</b>

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