

# The contribution of global mountains to the latitudinal diversity gradient

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## 1 **Abstract**

2 The latitudinal diversity gradient (LDG) is widely attributed to be the result of factors such as time, area, and  
3 energy. Although these factors explain most of the variation in lowlands, they fail in mountainous systems,  
4 which are biodiversity hotspots that may contribute meaningfully to the strength of the pattern following  
5 different evolutionary pathways. However, because lowlands cover the largest portion of the total land, they  
6 may have overshadowed the contribution of mountains to the LDG, but no study has addressed this issue in  
7 previous macroecological analyses. Here, we propose that the LDG shows a stronger trend in mountain ranges  
8 due to their high species turnover, in spite of covering less than one third of the Earth's land. Using the  
9 geographical information for ~22000 species of terrestrial vertebrates, we show that worldwide mountains  
10 harbor the 40% of the global diversity, and when taking into account the area effect, we quantified that  
11 mountains harbor close to double the species inhabiting lowlands per unit area. Moreover, when we evaluated  
12 the LDG after accounting for area size, we found that species richness increased faster towards the Equator  
13 and was better predicted by latitude in mountains than in lowlands. Our findings challenge previously well-  
14 supported hypotheses that predict that those regions with greater area, time and energy accumulate more  
15 species richness, since mountains are geologically younger, exhibit less energy, and cover smaller areas than  
16 lowlands. Hence, mountains represent a paradox, which invites to reevaluate hypotheses regarding  
17 macroecological and evolutionary processes driving species diversity gradients.

18

## 19 **Introduction**

20 The increase in species diversity towards the Equator is one of the most consistent and well-known patterns in  
21 ecology (1, 2), yet its underlying drivers remain elusive. Area, energy, and time are among the factors that  
22 best explain the latitudinal diversity gradient (LDG), as more species are accumulated in older and larger areas  
23 with higher productivity, where diversification is promoted by low extinction rates or frequent speciation  
24 events (1–4). Mountains, however, represent a paradox, as they may harbor exceptional levels of biodiversity  
25 in small areas (5, 6), are characterized by low levels of productivity in high elevations (7), are often  
26 geologically younger than surrounding lowlands, and have had less time to be colonized by clades that could  
27 have undergone subsequent diversification (8). In fact, several mountain ranges such as the Andes, the Eastern  
28 Arc mountains, and the Indo-Pacific mountainous islands are well recognized as biodiversity hotspots (9–11).

29 Previous attempts to relate regional species richness with contemporary climate, net primary  
30 productivity, and topography have failed to explain the high levels of diversity observed in mountains (5, 12).  
31 This suggests that the relative influence of evolutionary processes determining spatial patterns of species  
32 richness are different regarding lowlands. The contrasting patterns of species turnover (or beta-diversity)  
33 between landforms could be a consequence of such differential influence. Though species segregation is  
34 higher in tropical latitudes, it is strikingly prominent in tropical mountains, likely as a result of the dramatic  
35 change in abiotic conditions between adjacent elevational thermal belts, which contrasts with the less extreme  
36 zonation in temperate regions (5). This high zonation in tropical mountains facilitates the strong replacement  
37 of almost entire communities over short geographical distances. Considering the smaller area of mountains,  
38 the species replacement along slopes of mountain ranges may result in a greater capacity to harbor more  
39 species per unit area and, in turn, generate a greater species packing when compared to the lowlands. Thus, a  
40 higher species turnover in tropical mountains might have an additive effect on the inherent increase of  
41 diversity towards low latitudes, leading to a more pronounced LDG. Although the association between

42 latitude and beta-diversity in mountains has been previously noticed (13, 14), the magnitude to which it may  
43 generate an additive effect causing a difference in the LDG in mountains has not yet been explored.

44 Here, we hypothesize that latitudinal gradients are much stronger in mountains than in lowlands as a  
45 result of species packing and turnover. Addressing this issue has been challenging because lowland areas are  
46 geographically larger, and when the effect of area is not accounted for, the importance of mountains in  
47 determining the overall patterns of species diversity may be overshadowed. We quantify the contribution of  
48 mountains to worldwide species richness in three groups of terrestrial vertebrates to test whether the LDG is  
49 steeper in mountains than in lowlands after accounting for area size.

50

## 51 **Results and Discussion**

52 To address this issue, we first evaluated the total contribution of mountains to global patterns of bird,  
53 amphibian, and mammal species richness (ca. 22,000 species). Using public data on the global distribution of  
54 each of these groups, we calculated the proportion of each species' distribution in mountains vs. lowlands  
55 based on two alternative definitions of mountains: 1) areas above 700 m, a consensus on elevational limits  
56 used in several studies, and 2) areas with "high ruggedness," a criterion based upon elevational differences  
57 within a given area (6). A species was considered mountainous if the proportion of its distribution in  
58 mountains was higher than a given threshold ( $T$ ), such that a threshold of  $T=0.5$  meant that a species was  
59 considered mountainous when at least 50% of its distribution range was in mountains. We quantified global  
60 species richness in each group of vertebrates using a  $T=0.5$  and examined the robustness of our results by  
61 calculating a confidence interval based on  $T=0.3$  and  $T=0.7$  (see details in Methods).

62 Worldwide, we found that mountains were disproportionately species-rich compared to lowlands  
63 when accounting for area. Based on the elevation-driven definition of a mountain and a threshold of  $T=0.5$ ,  
64 mountains occupied only 28.5% of emerged lands, yet they harbored as much as 39% of the world's diversity  
65 of terrestrial vertebrates. This net estimation of number of species translates to 1.6 times more species per unit  
66 area than lowlands (Fig. 1B, Table 1). These results held even when using  $T=0.7$ , a highly conservative

67 threshold for considering a species as mountainous, where mountains harbored 31.5% worldwide diversity  
68 (Table 1). By evaluating groups separately, mountains held 1.3, 1.4 and 2.4 more birds, mammals and  
69 amphibians species respectively per unit area than lowlands (Figs. 1C,D,E, Table 1). Patterns were stronger  
70 when defining mountains based upon ruggedness, where mountains represented only 18.5% of emerged lands,  
71 but still containing the 39% of terrestrial vertebrates biodiversity. In other words, mountains held 2.9 times  
72 more richness per unit area than lowlands ( $T=0.5$ , SI Appendix, Fig. S1 and Table S1). Our findings contrast  
73 with those of Rahbek et al (5), who recently reported that mountains shelter 87% of terrestrial vertebrate  
74 species. We believe this value corresponds to an overestimation, as they included in their calculations any  
75 species occupying tangential areas in mountains. In this sense, our estimates are more conservative, as we  
76 considered a species to be mountainous only when a significant proportion of its distribution felt in  
77 mountainous landscapes.

78         Heightened diversity in mountains could be explained by topographic and climatic heterogeneity (13),  
79 which act as barriers to dispersal favoring the segregation of species with restricted dispersal abilities, thereby  
80 magnifying beta-diversity, which in turns enhances gamma diversity (13, 15). This species segregation also  
81 reflects the effects of historical and evolutionary forces that have promoted lineage accumulation in mountain  
82 ranges (16, 17). Indeed, there is evidence that mountains have greater diversification rates than lowlands (18),  
83 likely resulting from differences in the relative influences of processes occurring in each of these landforms.  
84 For example, tectonic uplift probably offered new and unexplored arenas, ready to be colonized by lowland  
85 clades or temperate migrants (19), which in turn may undergo speciation through vicariance, facilitated by  
86 niche conservatism or ecological opportunity in new high elevation environments (20–22). High  
87 diversification rates in mountains could also be driven by lower extinction rates, as species may be less  
88 vulnerable to environmental changes given that they need to disperse shorter distances up or down slope to  
89 escape unsuitable areas compared to lowlands (17). Overall, the relative contribution of speciation versus  
90 extinction rates to differences in diversification rates between mountains and lowlands needs to be evaluated  
91 in future studies.

92           Given the extraordinary species richness of mountains, we tested whether the strength of the  
93 latitudinal gradient in mountains is different from that in lowlands, when we take into account the area. We  
94 evaluated the relationship between species richness and latitude in each landform for all three vertebrate  
95 groups combined and separately. Species richness was estimated at a finer pixel resolution (10km x 10km;  
96 Fig. 1A) than previous macroecological works (e.g. ~110km x 110km). This enabled us to minimize the  
97 mixing of mountain and lowland areas within the same pixel, and to reduce mountain underrepresentation  
98 resulting from their low extension (see Methods). To control for spatial autocorrelation, we implemented a  
99 Monte Carlo procedure, where, for each of 1000 iterations, we randomly selected 1000 pixels located in  
100 mountains and 1000 pixels located in lowlands across the globe, and estimated the slope ( $\beta$ ) and coefficient of  
101 determination ( $R^2$ ) of the linear regression predicting species richness from latitude.

102           Using the elevation-based definition of mountains, we found a negative relationship between species  
103 richness and latitude for both landforms, but slopes ( $\beta$ ) and coefficients of determination ( $R^2$ ) were  
104 significantly higher for mountains (ANOVA:  $P < 0.001$ ; Fig. 1F, SI Appendix, Fig. S2 and Table S2). In other  
105 words, species richness increased faster towards the Equator and was better predicted by latitude in mountains  
106 than in lowlands. Remarkably, the latitudinal point where the slopes of the two models crossed, i.e., where  
107 species richness becomes higher in mountains than in lowlands towards the Equator, roughly corresponded to  
108 the subtropical-temperate latitudinal limit (especially in birds and mammals). A stronger latitudinal gradient in  
109 mountains supports the untested hypothesis put forth by Simpson (14), who claimed that “where there are  
110 latitudinal gradients, these are additive with topographic gradients, the two accounting for most of the  
111 pattern.” Our findings also concur with patterns reported by Fjelds  (23), where mountains were particularly  
112 species-poor in temperate latitudes, especially above 20-40° latitude. When using the ruggedness-based  
113 definition of mountains, the slopes describing the LDG were apparently parallel and never crossed, although  
114 they were statistically steeper for lowlands than for mountains ( $P < 0.001$ ; SI Appendix, Fig. S3 and S4).  
115 However, as in the elevation-based analysis, latitude explained a higher fraction of the variance in species  
116 richness in mountains than in the lowlands ( $P < 0.001$ ; SI Appendix, Table S3).

117           The fact that differences between mountains and lowlands were more conspicuous using the  
118 elevation-based definition of mountains suggests that elevation is more strongly related to the underlying  
119 processes determining the LDG in mountains than topographic complexity alone. Specifically, variables  
120 correlated with elevation, such as oxygen concentration and temperature, are likely to limit vertebrate  
121 physiological responses along elevation gradients but not across topographical heterogeneity. Indeed, the fact  
122 that mountains showed higher diversity than lowlands below the subtropical-temperate latitudinal limit  
123 suggests that there might be region-specific processes shaping patterns of vertebrate species richness in the  
124 tropics. This finding fits with the idea that “mountain passes are higher in the tropics” (24, 25), which  
125 provides a powerful mechanistic explanation for why conditions in tropical mountains generate an additive  
126 effect that magnifies the latitudinal gradient of species richness. D. H. Janzen (24) suggested that  
127 topographical barriers are more efficient in tropical than in temperate latitudes because tropical species are  
128 expected to have narrower thermal tolerances in response to higher thermal stability in tropical mountains.  
129 Narrow thermal tolerance increases the cost of dispersal across thermal belts, which may reduce gene flow  
130 between tropical populations and eventually may facilitate allopatric speciation (21, 25, 26).

131           When evaluating each group separately, mammals and birds exhibited similar patterns to the overall  
132 trend ( $P < 0.001$ ; Figs. 1C and E) but in amphibians the rate of increment in species richness towards the  
133 Equator was similar between landforms ( $P < 0.001$ ; Fig. 1D, SI Appendix, Fig. S2 and Table S2). This finding  
134 could result from differences in dispersal abilities and contrasting physiological features between ectotherms  
135 (amphibians) and endotherms (birds and mammals), which in turn is expected to affect their spatial  
136 distribution. Unlike endotherms, the major restriction for amphibian distribution at high elevations is not  
137 determined by thermal tolerance but rather by humidity and ultraviolet radiation (27, 28). If so, changes in  
138 temperature associated with mountain topographic heterogeneity should be more efficient barriers for  
139 mammals and birds than for amphibians, therefore explaining the different patterns in the LDG observed  
140 between ectotherms and endotherms.

141 As mountainous regions harbor most of the range-restricted species occurring worldwide (11, 17), one  
142 may wonder whether our results were affected by the predominance of this group of species. To address this  
143 issue, we evaluated the relationship between species richness and latitude by partitioning species into range  
144 size quartiles (12, 29). Patterns of species richness along the latitudinal gradient for range-restricted  
145 (narrowest ranging 25%) and widespread (widest ranging 25%) species were alike (SI Appendix, Fig. S5),  
146 indicating that our findings were not biased by differences in species' spatial distribution between landforms.  
147 We also evaluated whether our results were driven by region-specific patterns which could be generating the  
148 global pattern. For instance, the Andes Cordillera is well-known to concentrate high levels of diversity,  
149 especially of range-restricted species, compared to other large mountain systems like the Himalayas or any  
150 other system in the Eastern Hemisphere (11, 30). We therefore analyzed our data by accounting only for  
151 species occurring either in the New World or in the Old World, yet both regions showed congruent results  
152 (Fig. 2, SI Appendix Fig. S6), supporting the idea that our findings correspond to a generalized trend across  
153 the globe.

154 Overall, we show that mountains harbor a higher diversity per unit area and exhibit a steeper LDG  
155 than lowlands. Our results have critical insights for the understanding of the LDG, one of the most striking  
156 patterns in the distribution of biodiversity. In particular, the fact that species richness of terrestrial vertebrates  
157 per unit area in mountains surpassed that of lowlands challenges the time-area hypothesis, where older and  
158 larger areas with historically higher energy availability are more likely to accumulate greater diversity (1, 31,  
159 32). Although we do not provide an explicit test of this hypothesis, our results contrast with its predictions in  
160 different ways. First, mountains contributed nearly 40% of the world's gamma diversity, despite covering less  
161 than one third of the available terrestrial area. Second, mountains tend to have lower energy in terms of  
162 primary productivity than lowlands. Third, available time for colonization and diversification in mountains is  
163 likely to be lower than in surrounding lowlands, not only due to relatively recent orogenic processes, but also  
164 because glacial cycles have recurrently erased biotas of high elevations in tropical and temperate mountains  
165 (33). It is therefore essential to integrate the effect of time since colonization in future studies evaluating LDG,



166 because it may influence the net cumulative diversity in mountains and lowlands. Doing so would require  
167 geological and paleoclimatic information combined with data on orogeny, which are not available yet. Until  
168 then, our results shed reasonable doubt on the explanatory power of the time-area hypothesis.

169         If the relative influence of diversification processes associated with spatial heterogeneity, dispersal  
170 mechanisms, and reproductive isolation varies from lowlands to mountains (17, 30, 33), evaluating these two  
171 landforms without any distinction may obscure the underlying processes determining global patterns of  
172 species richness. We therefore need to recognize a possible effect of region and control for the effect of area  
173 to avoid overshadowing the influence of mountains in macroecological analyses. When considering that  
174 tropical mountains are among the most diverse yet threatened systems by human activities and climate change  
175 worldwide (34, 35), our results have important implications in conservation biology. Given the exceptional  
176 levels of species richness in mountains, if we want to understand the processes that generate *worldwide*  
177 diversity, we must first understand the processes that generate overall *mountain* diversity.

178

## 179 **Methods**

180 **Definitions of mountains.** We selected two criteria proposed in the literature to define mountains: one based  
181 on an elevational limit threshold and another based on ruggedness (6). Based on a landmass grid of 10 km x  
182 10 km, we classified each pixel as either mountain or lowland following each of these two criteria. The  
183 elevation criterion defined mountains as areas with elevation above 700 masl. Using this elevation limit and  
184 creating a mask based on a digital elevation model (SRTM Digital Elevation Database v4.1:  
185 <http://www2.jpl.nasa.gov/srtm/>), we found that the global area of mountains represented 28.5 % of the total  
186 land area. For ruggedness, we used the raster layer of mountains generated by Körner et al. (6). Ruggedness is  
187 defined as the maximal difference in elevation among neighboring grid points, where mountains were  
188 determined as pixels with at least 200 meters of ruggedness. This definition, however, may include isolated  
189 pixels that are not part of mountain ranges, usually at low elevations. To correct for this potential bias, we

190 considered only pixels with an elevation above 200 meters (around 30% of pixels were discarded). Under this  
191 criterion, the global area of mountains represented 18.5% of total land area.

192 Both definitions show different landscape attributes that impact particular ecological and  
193 physiological traits (36). A classification of mountains based on elevation alone inflates the influence of  
194 variables like changes in air pressure, oxygen concentration, temperature, and UV radiation along elevation  
195 gradients, all of which demand physiological mechanisms that constrain animal distribution at high altitude.  
196 The downside is that thermal belts are not comparable for all latitudes and mountain systems, because features  
197 such as air currents, distance to the ocean, and topography also influence abiotic variables. Ruggedness, on the  
198 other hand, captures topographical complexity, but includes rough terrain at low elevations and excludes flat  
199 land at high elevations (e.g., the Andean plateaus in Colombia and Bolivia, the Rocky Mountains in the USA,  
200 or the Tibetan Plateau). Thus, ruggedness does not correlate with physical factors interacting with vertebrate  
201 physiological traits. Furthermore, ruggedness acts as a proxy of slope, which is more important in young  
202 mountain systems than in older ones, where erosion may have worn away steep slopes. For these reasons, we  
203 expected each definition to show different results given their features. For instance, defining mountains based  
204 on elevation may reflect climatic restrictions on species distribution, whereas doing so based on ruggedness  
205 emphasizes how physical attributes interact with species dispersal across barriers in mountainous areas. When  
206 evaluating the map congruence between both definitions, we found a match in 77% of the pixels, where the  
207 remaining 23% corresponded mainly to areas below 3000 masl. A map illustrating discrepancies between  
208 mountain areas according to both definitions is shown in SI Appendix, Fig. S7.

209 Although defining mountains as areas above 700 masl may be seen as arbitrary, any other threshold  
210 chosen would be as arbitrary as this one. This issue has been discussed in detail (37), and although different  
211 elevation limits have been used to differentiate mountains from lowlands, a limit of 1000 masl is the one most  
212 frequently used. Nonetheless, it has also been recognized that several mountain systems occur at elevations  
213 below 1000 masl in tropical areas (23), between 500 and 700 masl (37). We therefore present our results using

214 the elevation thresholds of 700 masl and quantified the deviation of our estimates based on elevation limits of  
215 500 and 1000 masl (see next section).

216 **Quantifying global mountain diversity.** To evaluate the contribution of mountains to worldwide species  
217 richness in terrestrial vertebrates, we assembled a comprehensive database which maps species distribution for  
218 birds, amphibians and mammals at the finest resolution ever performed at the worldwide scale (10 km x 10  
219 km). To do so, we quantified the extent to which the distribution range of each species overlaps with the  
220 masks for mountain areas obtained using the two definitions of mountains, respectively. We used expert  
221 distribution maps for birds (BirdLife International <http://www.birdlife.org/datazone/home>, accessed October  
222 2014), amphibians, and mammals (IUCN Digital distribution maps <http://www.iucnredlist.org/technical->  
223 [documents/spatial-data](http://www.iucnredlist.org/technical-documents/spatial-data), accessed October 2014). For birds, we only quantified the distribution of breeding  
224 areas of migratory species and excluded 238 marine species belonging to 10 families (Alcidae, Procellariidae,  
225 Spheniscidae, Stercorariidae, Laridae, Diomedidae, Oceanitidae, Hydrobatidae, Sulidae, and Phaethontidae).

226 An issue pointed out in several macroecological studies at regional and global scales is the fact that  
227 expert maps for some species may have coarse limits and include zones outside the known distribution (for  
228 example, valleys or mountain peaks) (38). To reduce this bias and partially solve this problem at the scale and  
229 resolution of our study, especially in the case of birds, we constrained distribution maps to the known  
230 elevation range of each species, setting minimum and maximum elevation according to information in the  
231 Handbook of Birds of the World (39). We rasterized each species map to a 10 km x 10 km resolution using a  
232 WGS84 coordinate system. In some cases, mammals and amphibian species showed distribution ranges that  
233 were not detectable at the resolution used. In these specific cases, we rasterized their maps to 1 km x 1 km. In  
234 total, we used 21,741 species (10,186 birds, 6,266 amphibians, and 5,289 mammals). All procedures were  
235 undertaken using the libraries `mapproj` (40) and `raster` (41) in R Software (42).

236 For each species and each mountain definition, we quantified the proportion of their distribution that  
237 overlapped with mountains using the rasterized maps separately (ranged from 0 for species showing a  
238 distribution entirely in the lowlands to 100% for species showing a distribution entirely in mountains). We

239 defined a threshold ( $T$ ) for species to be considered as montane, which refers to the minimum proportion of  
240 each species' distribution overlapping with mountains. For example, a threshold of  $T=0.5$  means that we  
241 considered a species to be montane when at least 50% of its distribution overlapped with mountains. To  
242 evaluate the sensitivity of our results to a certain threshold  $T$ , we performed all analyses using three different  
243 thresholds,  $T=0.3$ ,  $T=0.5$ , and  $T=0.7$ . We considered that  $T=0.5$  reflected the mean number of species in  
244 mountains and that using  $T=0.3$  and  $T=0.7$  reflected the range of standard error around this number  
245 ( $T=0.5\pm 0.2$ , Fig. 1, Table 1, SI Appendix, Fig. S1 and Table S1). When using elevation-based definition of  
246 mountains, we further evaluated the sensitivity of this analysis to three different elevation limits (500, 700,  
247 and 1000 masl). As expected, we found that species richness in mountains decreased as the elevation  
248 threshold ( $T$ ) increased; however, mountain area also diminished such that estimates of species per unit area  
249 did not show significant differences when changing elevation thresholds (SI Appendix, Fig. S8).

250 **Patterns of species richness along latitudinal gradients.** To assess patterns of species richness along  
251 latitudinal gradients when controlling for area, we evaluated the relationship between species richness and  
252 latitude in either mountains and lowlands for birds, mammals and amphibians. We also performed the same  
253 analysis by summing the richness of the three groups simultaneously. Based on the rasterized maps of the  
254 distribution of the 21,741 vertebrate species, we generated a global map of species richness using a grid of 10  
255 km x 10 km (around eight million pixels). To avoid spatial autocorrelation, we implemented a Monte Carlo  
256 procedure where we generated a random distribution of pixels where, for each of 1000 iterations, we  
257 randomly selected a sample of 1000 pixels located in mountains and 1000 pixels in lowlands. Because the  
258 area covered by land at northern latitudes is greater than in the tropics or at southern latitudes and corresponds  
259 mainly to lowland areas (SI Appendix, Fig. S9), we controlled for differences in area between tropical and  
260 temperate zones. To do so, we forced each subset of 1000 pixels to contain 500 pixels from tropical latitudes  
261 (below 23° latitude) and 500 pixels from temperate latitudes (above 23° latitude). We performed this  
262 procedure for mountain layers based on elevation and ruggedness. Finally, based on these subsamples, we ran  
263 a linear regression predicting local species richness against latitude and extracted the slope ( $\beta$ ) and the

264 coefficient of determination ( $R^2$ ) for mountains and lowlands separately. We compared the distributions of  
265 these two parameters between mountain and lowlands using an ANOVA ( $N = 1000$ ). In addition, we tested  
266 for bias considering groups of species with different range size (from narrow-ranging to wide-ranging  
267 species), for which we divided the complete species pool in four 25% quantiles based on their distribution  
268 size, and performed the same analyses for each quantile (SI Appendix, Fig. S5). Finally, we also tested by  
269 differences among the main mountain ranges separated by continent that may exhibit region-specific patterns.  
270 For this, we ran the same regression analyses by dividing the global species pool in species in the same four  
271 quantiles but separating them in species occurring in the New World or the Old World (Fig. 2, SI Appendix,  
272 Fig. S6).

273

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288 **References**

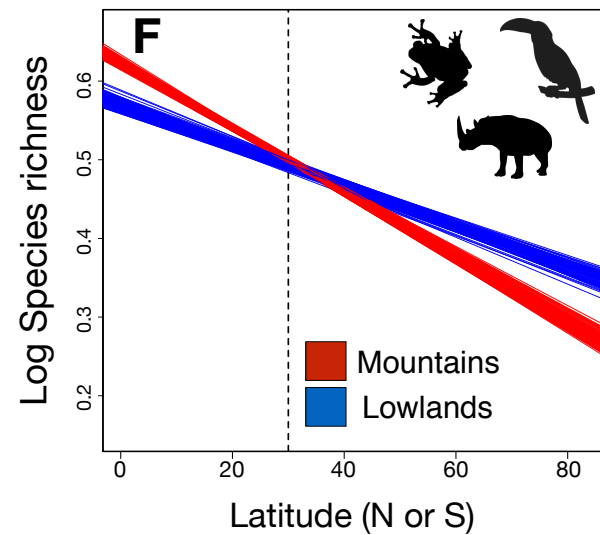
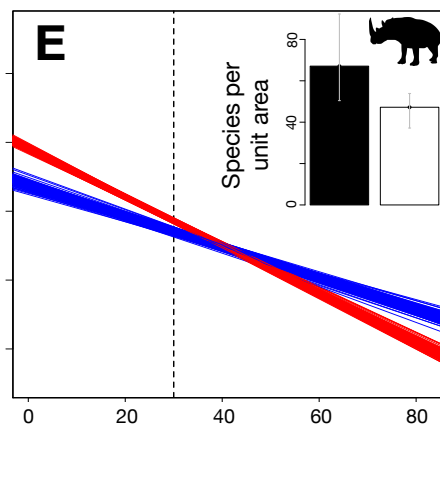
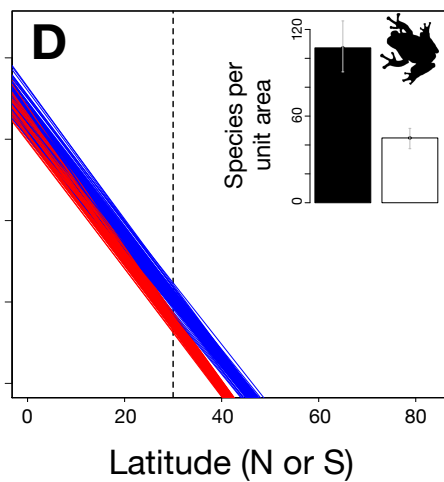
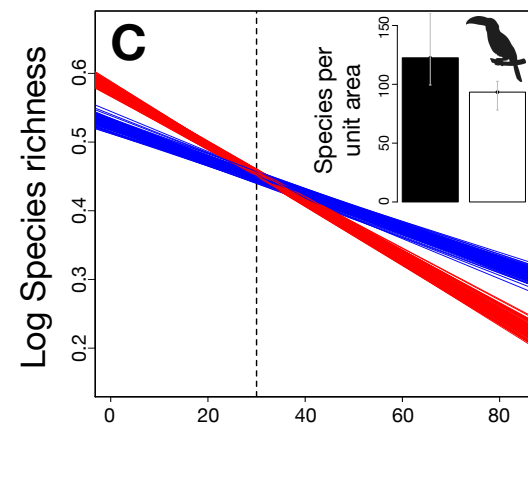
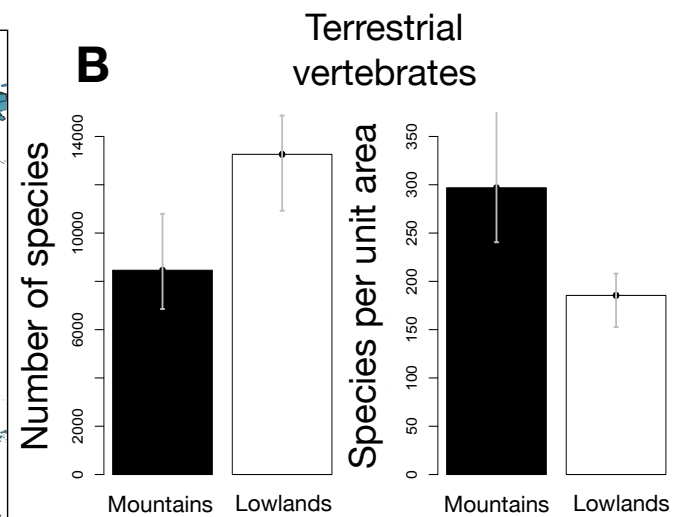
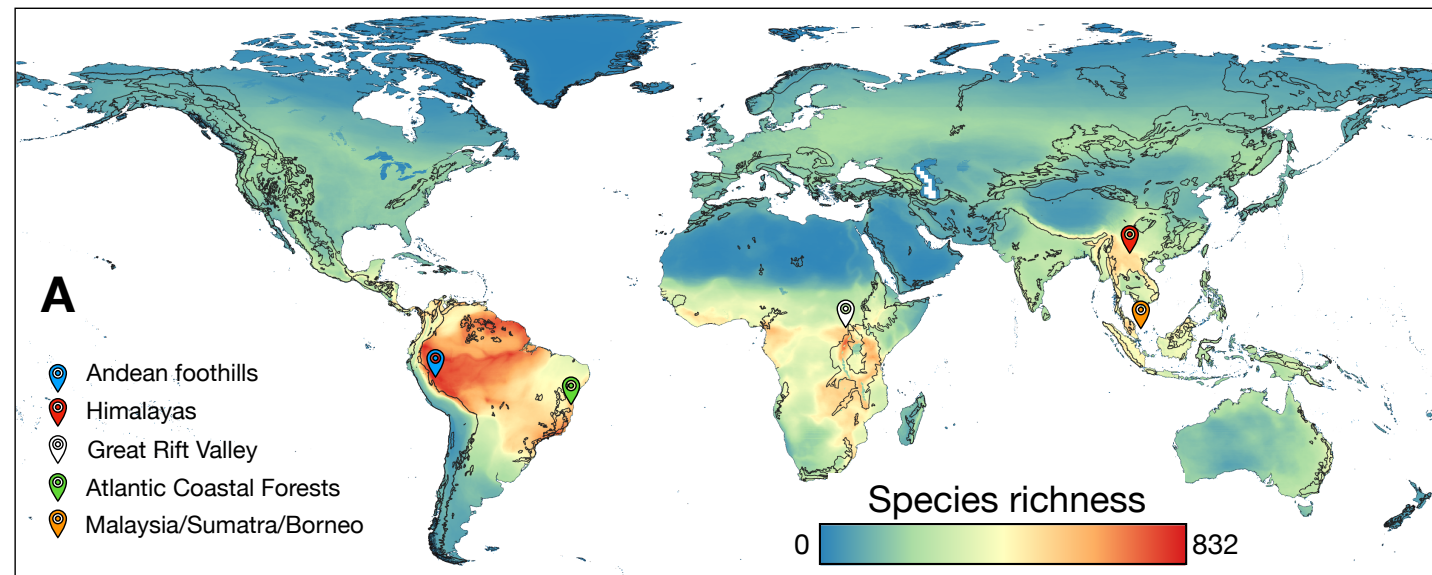
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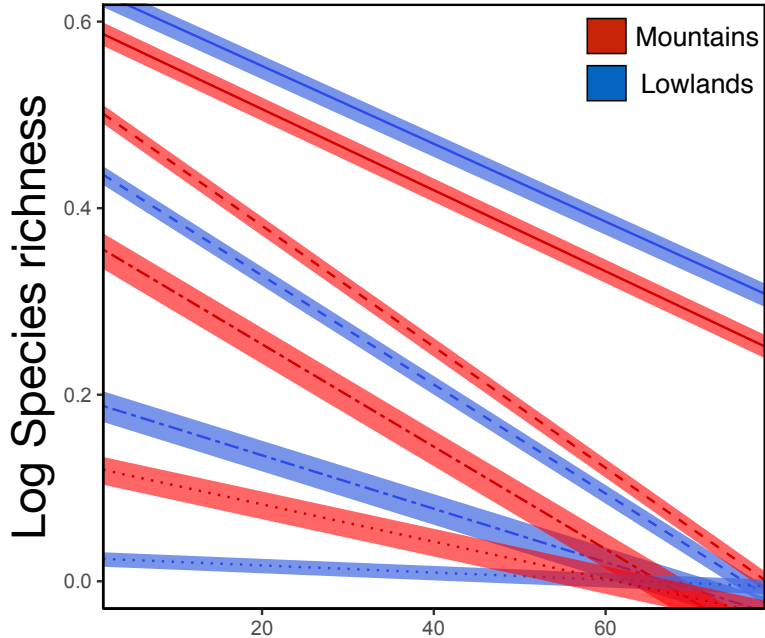
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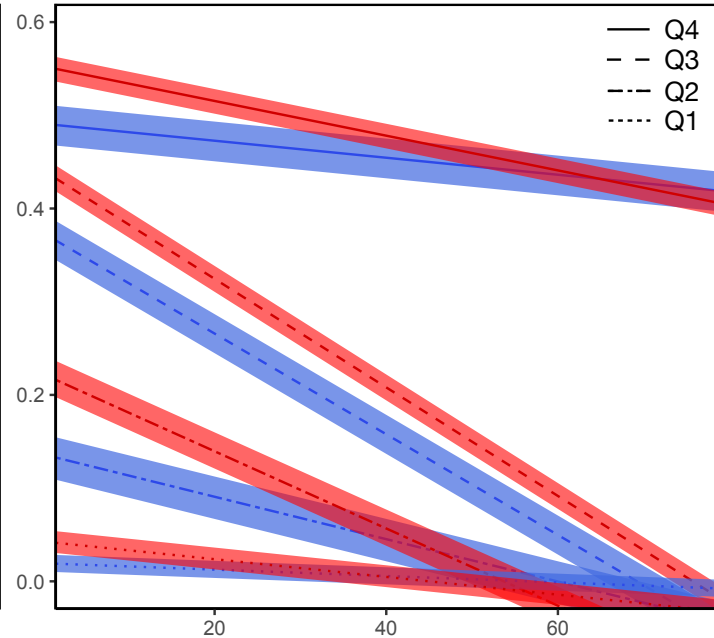
373 **Fig. 1.** Global patterns of species richness in mountains vs. lowlands. (A) Species richness map of the three  
374 groups of terrestrial vertebrates (birds, mammals, and amphibians). Mountains regions are outlined by a black  
375 line following the inventory of the World's mountains from the Global Mountain Biodiversity Assessment  
376 (GMBA, <http://www.mountainbiodiversity.org>). Excepting the Amazon, highest values of species richness are  
377 associated mainly with tropical mountain systems, as exemplified by the color marks highlighting five  
378 mountain ranges (Andean foothills, Himalayas, Great Rift Valley, Atlantic Coastal Forest and mountains in  
379 Malaysia, Sumatra, and Borneo). (B) Differences in the contribution of mountains (black bars) and lowlands  
380 (white bars) to the total species richness combining the three groups of terrestrial vertebrates based on an  
381 elevation criterion for defining mountains. The bars in (B) represent the total number of species and the  
382 number of species per unit area for all three groups, and separately for (C) birds (D) amphibians, and (E)  
383 mammals. In each panel, bar height corresponds to estimations using a  $T=0.5$  and intervals (gray vertical line)  
384 correspond to values generated by varying  $T$ , the threshold for defining a species distribution as being in  
385 mountains vs. lowlands ( $T= 0.5\pm 0.2\%$ ,  $T=0.3\%$  and  $T= 0.7\%$  - values in Table 1). (F) Patterns of species  
386 richness along the latitudinal gradient for mountains (red) and lowlands (blue) when area is controlled for and  
387 using an elevation criterion to define mountains; analyses were performed for all vertebrates (F), and  
388 separately for (C) birds (D) amphibians, and (E) mammals. Trend lines were extracted from 100 linear models  
389 constructed using 1000 random pixels for both mountains and lowlands. The dotted black line represents  $30^\circ$   
390 latitude, the subtropical-temperate limit where the average richness per latitude point is higher in mountains.  
391 Silhouettes were taken from PhyloPics (credits to Will Booker, FJDegrance, and Zimices).

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### New World



### Old World



Latitude (N or S)

393 **Fig. 2.** Species richness patterns by range size quartiles of terrestrial vertebrates richness (birds, amphibians,  
394 and mammals) in the New World and the Old World. Analysis was performed using a resample method to  
395 control by area and using an elevation criterion to limit mountains. Species were divided in four geographic  
396 range size quartiles, from the narrowest ranging species (1<sup>st</sup>, 0-25%) to the widest ranging (4<sup>th</sup>, 75-100%), and  
397 the line pattern represents each quartile: solid line (1<sup>st</sup> quartile), dashed line (2<sup>nd</sup> quartile), dash-dotted line  
398 (3<sup>th</sup> quartile), and dotted line (4<sup>th</sup> quartile). Envelopes around each line show the 95% confidence interval  
399 generated by extracting the trend lines from 1000 linear models based on a random sample of 1000 pixels for  
400 mountains and lowlands separately for mountains (red) and lowlands (blue) in each quartile and continent.

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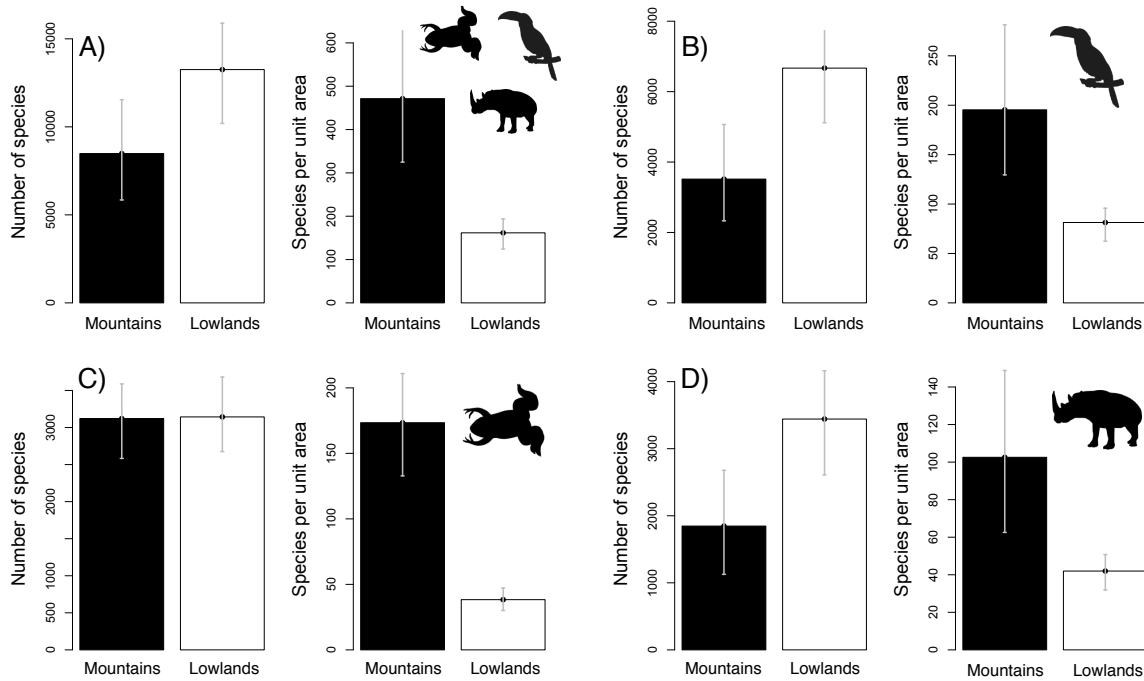
402 **Table 1. Estimation of mountain and lowland contribution to the total species richness of birds,**  
 403 **amphibians, and mammals (gamma diversity).**

Group	Proportion of mountain distribution ( $T$ )	Mountain species	Lowland species	Mountain species per unit area	Lowland species per unit area
All groups	0.3	10796 (50%)	10924 (50%)	378.80	152.78
	0.5	8460 (39%)	13260 (61%)	296.84	185.45
	0.7	6855 (32%)	14865 (68%)	240.52	207.90
Birds	0.3	4578 (45%)	5590 (55%)	160.63	78.18
	0.5	3492 (34%)	6676 (66%)	122.53	93.37
	0.7	2835 (28%)	7333 (72%)	99.47	102.56
Amphibians	0.3	3588 (57%)	2676 (43%)	125.89	37.43
	0.5	3056 (49%)	3208 (51%)	107.23	44.87
	0.7	2583 (41%)	3681 (59%)	90.63	51.48
Mammals	0.3	2630 (50%)	2658 (50%)	92.28	37.17
	0.5	1912 (36%)	3376 (64%)	67.09	47.22
	0.7	1437 (27%)	3851 (73%)	50.42	53.86

404 Values are given for different thresholds ( $T$ ) for defining a mountain species ( $0.5 \pm 0.2\%$ ), and based on an  
 405 elevation-based mountain definition. Reported are the number of species in mountains and lowlands and the  
 406 respective percentage is given in brackets.  
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409 **Supplementary information**

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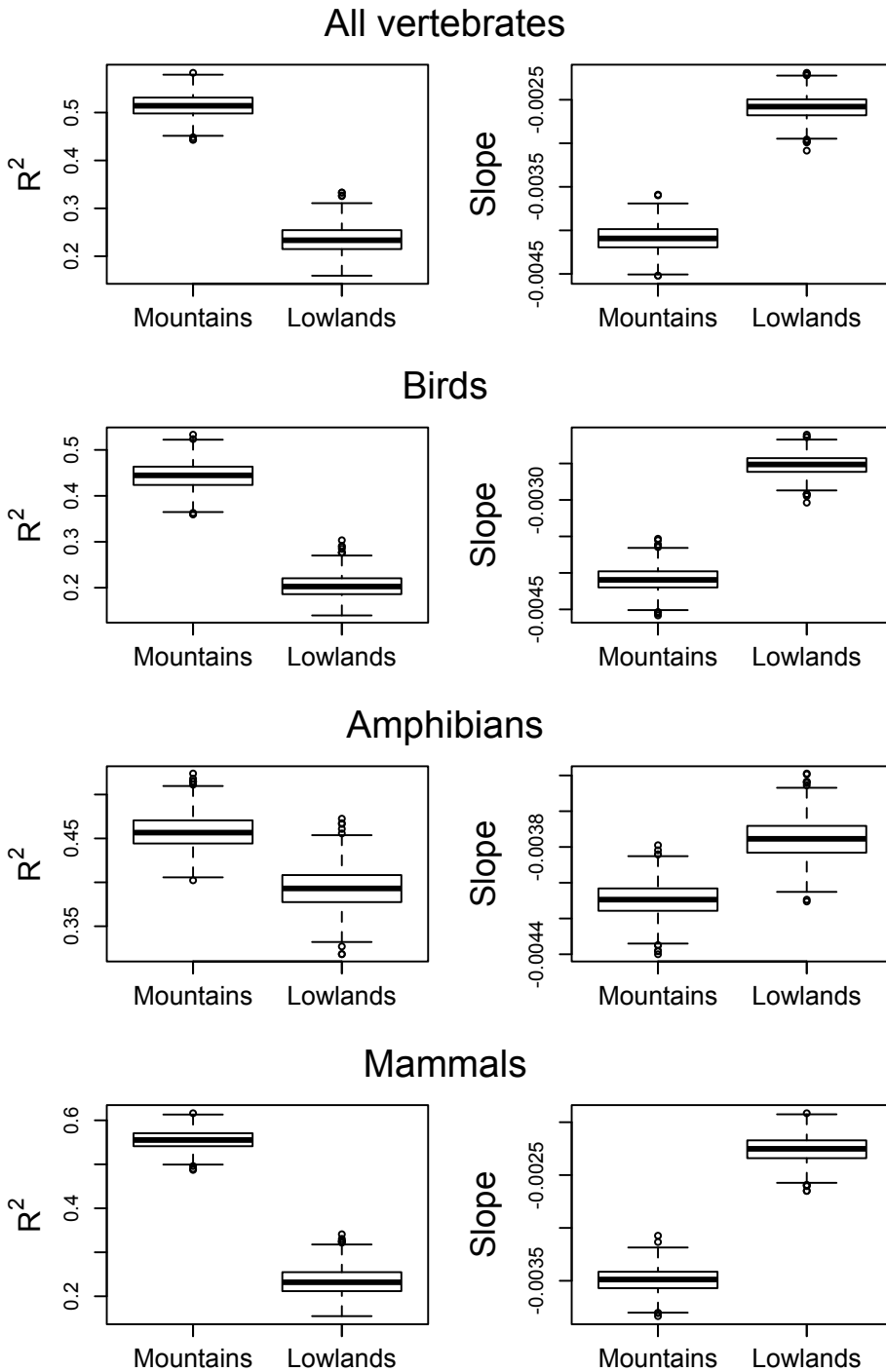
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413 **Fig. S1.** Differences in the contribution of mountains (black bars) and lowlands (white bars) to the total species richness  
414 of terrestrial vertebrates (global gamma-diversity) based on a ruggedness criterion to distinguish mountains from  
415 lowlands. The bars represent the total number of species (gamma diversity) and the number of species per unit area for  
416 all vertebrates (A), birds (B), amphibians (C), and mammals (D). In each panel, bar height corresponds to estimations  
417 using a  $T=0.5$  and intervals correspond to the values generated based on  $T=70\%$  and  $T=30\%$  ( $T=50\pm 20\%$ ).

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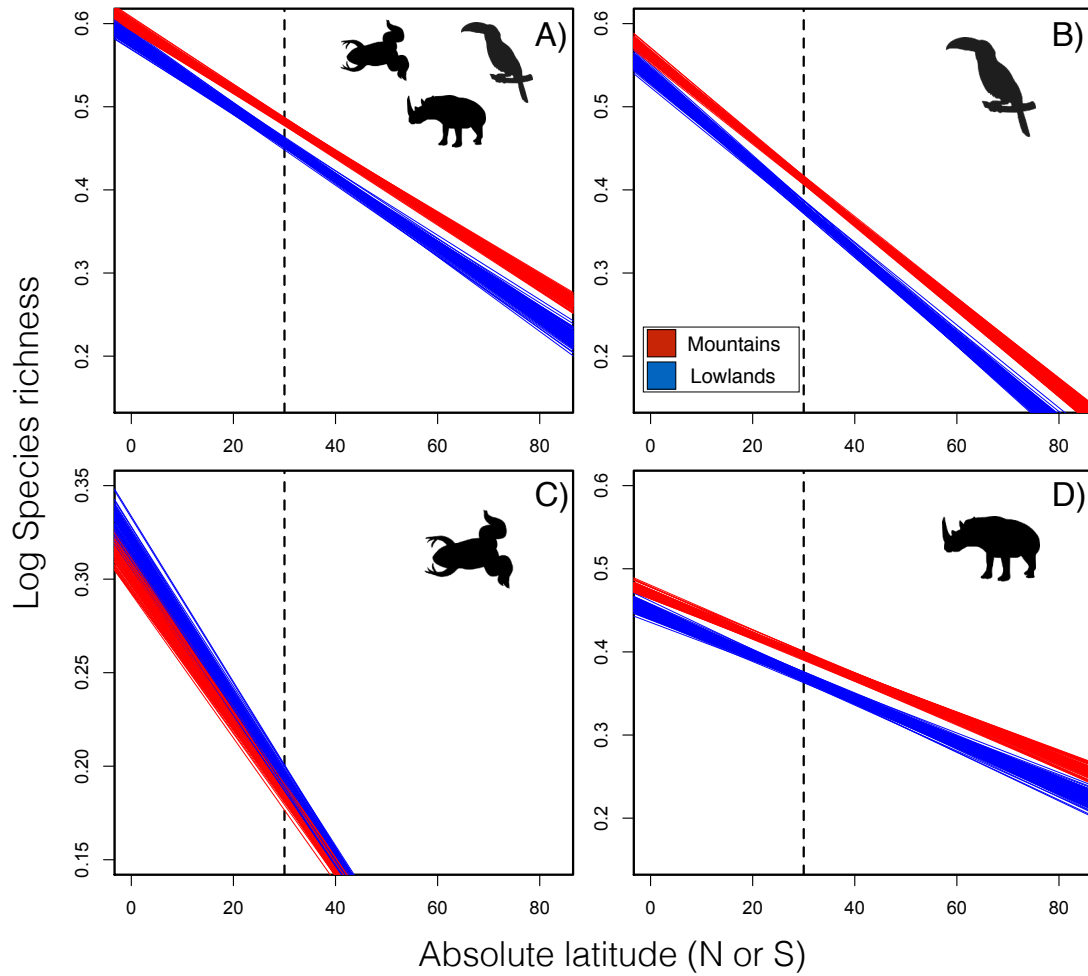


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422 **Fig. S2.** Boxplot illustrating differences in the coefficient of determination ( $R^2$ ) and the slope ( $\beta$ ) of the linear regression  
423 predicting species richness against latitude based on a Monte Carlo procedure (1000 iterations) for mountains and  
424 lowlands, and using an elevation-based definition of mountain for all vertebrates (A), birds (B), amphibians (C) and  
425 mammals (D).





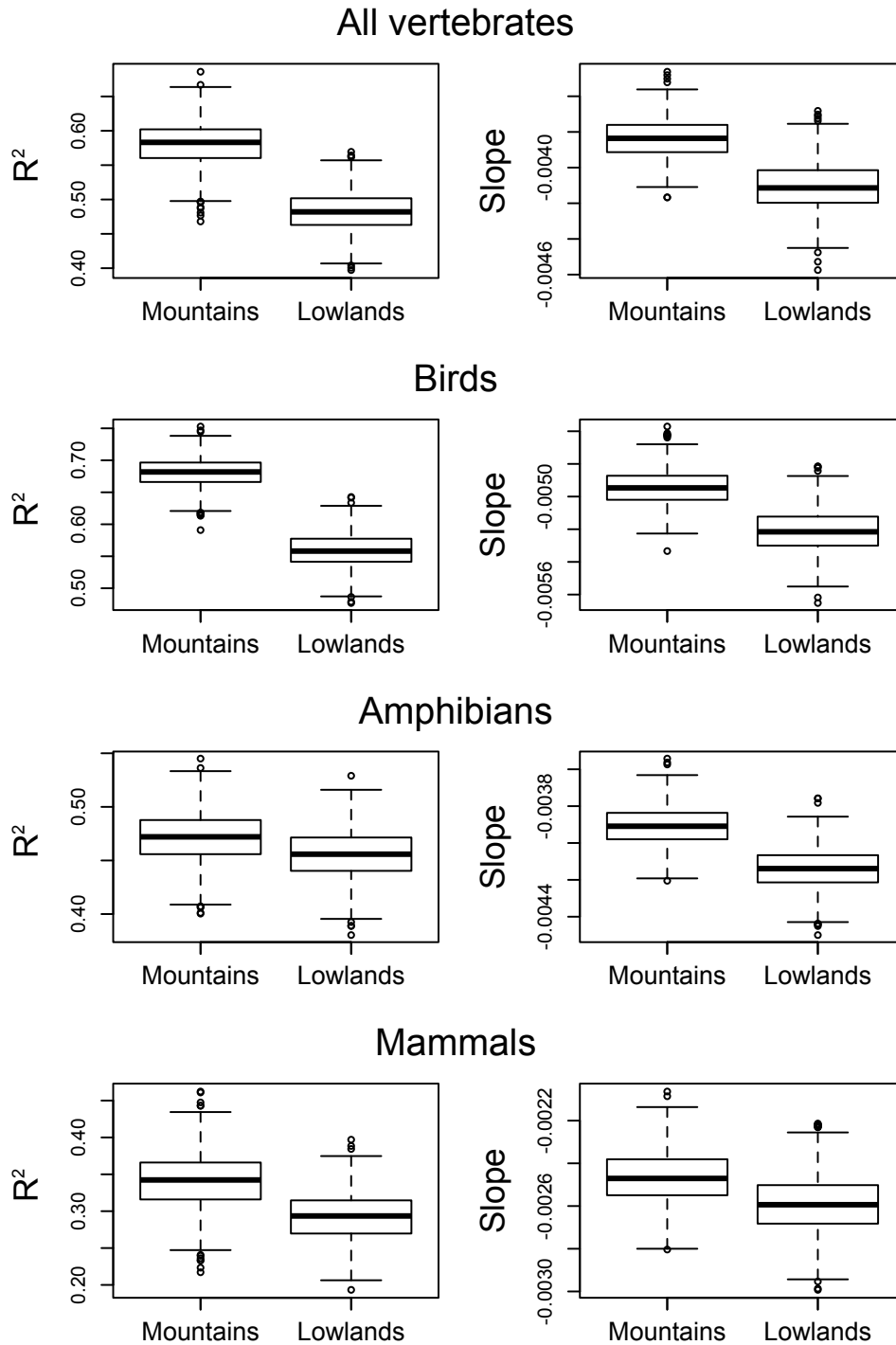
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428 **Fig. S3.** Patterns of species richness along the latitudinal gradient for mountains (red) and lowlands (blue) controlling by  
429 area, using a ruggedness criterion to limit mountains for all vertebrates (A), birds (B) amphibians (C), and mammals (D).  
430 Trend lines were extracted from 100 linear models based on a random sample of 1000 pixels for mountains and lowlands  
431 separately. The dotted black line represents 30° latitude, which represents the subtropical-temperate limit.

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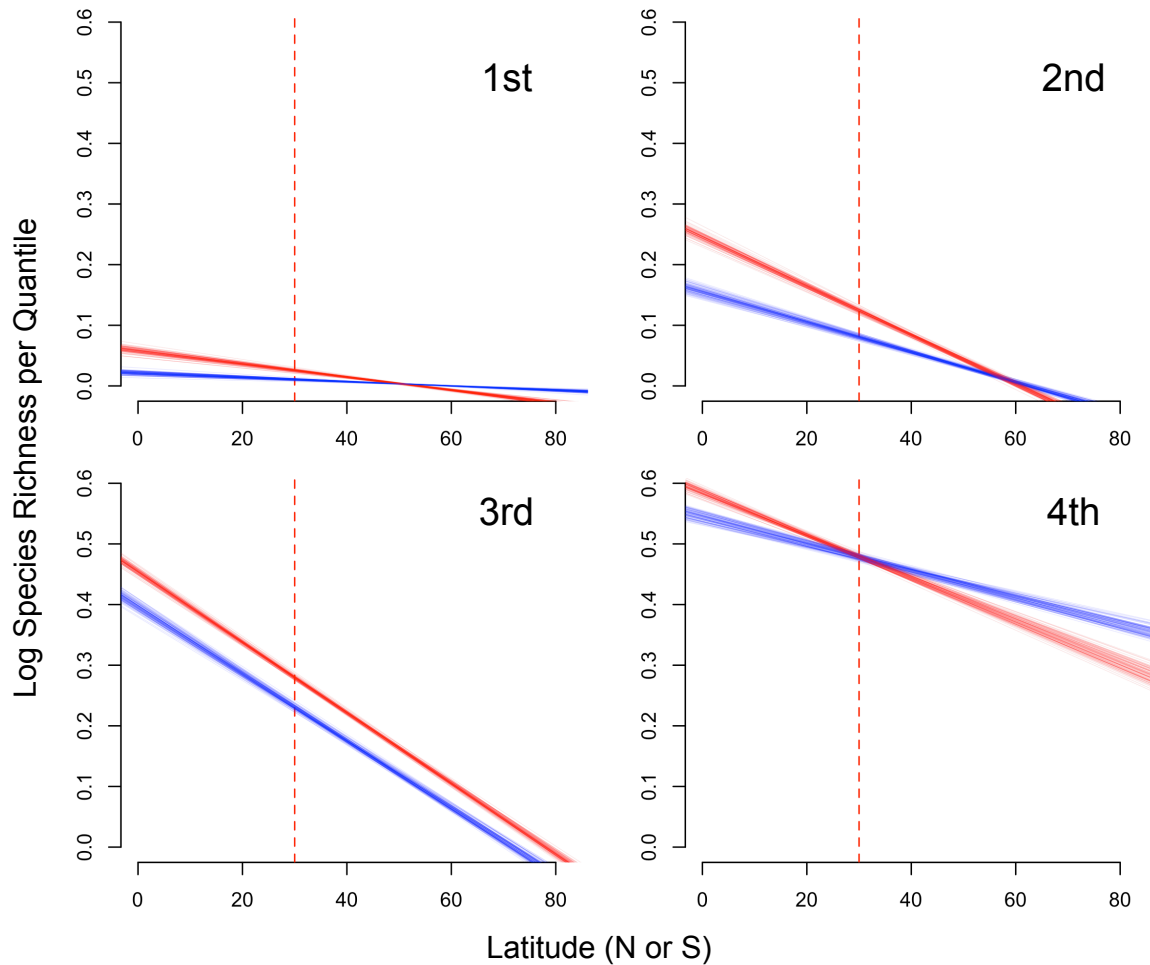
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436 **Fig. S4.** Boxplot illustrating differences in the coefficient of determination ( $R^2$ ) and the slope ( $\beta$ ) of the linear regression  
437 predicting species richness against latitude based on a Monte Carlo procedure (1000 iterations) for mountains and  
438 lowlands, and using an ruggedness-based definition of mountain for all vertebrates (A), birds (B), amphibians (C) and  
439 mammals (D).

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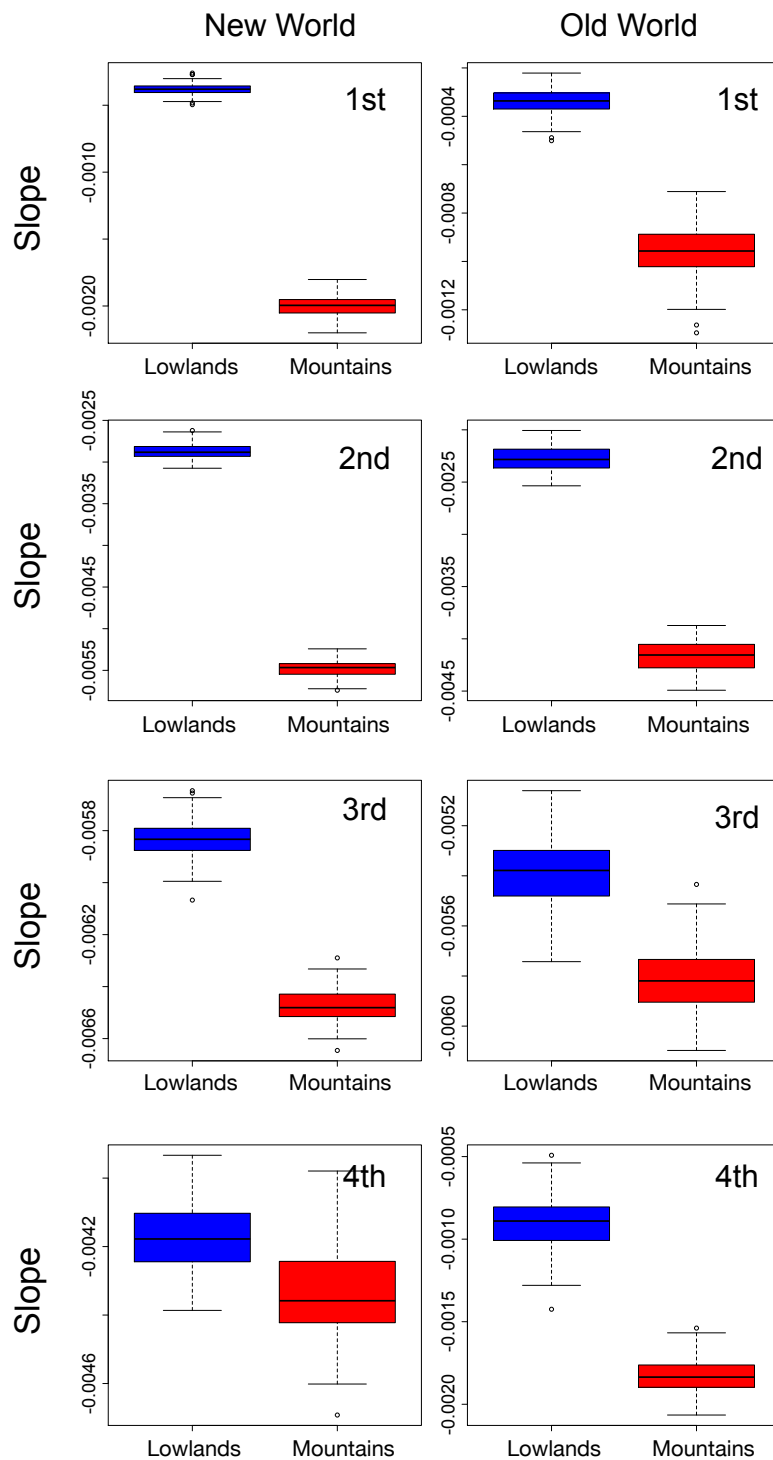
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444 **Fig. S5.** Species richness patterns by range size quartiles of terrestrial vertebrates richness (birds, amphibians, and  
445 mammals) along the latitudinal gradient for mountains (red) and lowlands (blue), controlling by area and using an  
446 elevation criterion to limit mountains. Each panel corresponds to a group of species divided in four quartiles according to  
447 their distribution range size, from the most restricted range species (1<sup>st</sup>, 0-25%) to the most widespread range species (4<sup>th</sup>,  
448 75-100%). Trend lines were extracted from 100 linear models based on a random sample of 1000 pixels for mountains  
449 and lowlands separately. The dotted black line represents 30° latitude, which represents the subtropical-temperate limit.

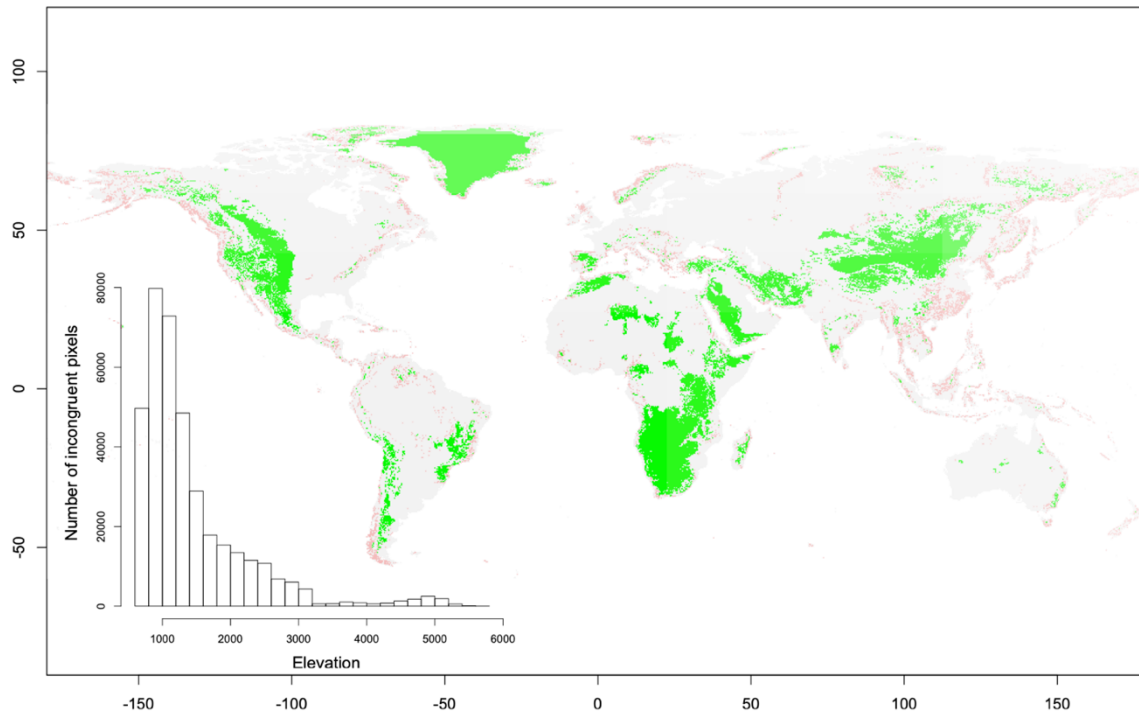
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453 **Fig. S6.** Boxplots of range size quantiles comparisons (four quantiles of 25%), illustrating differences in slopes ( $\beta$ ) from  
454 linear regression predicting species richness against latitude between mountains (red) and lowlands (blue) based on a  
455 Monte Carlo procedure (1000 iterations). Analyses were performed separating pixels falling in the New World and Old  
456 World and using an elevation-based definition of mountain for all vertebrates. In all cases, significant differences were  
457 detected.



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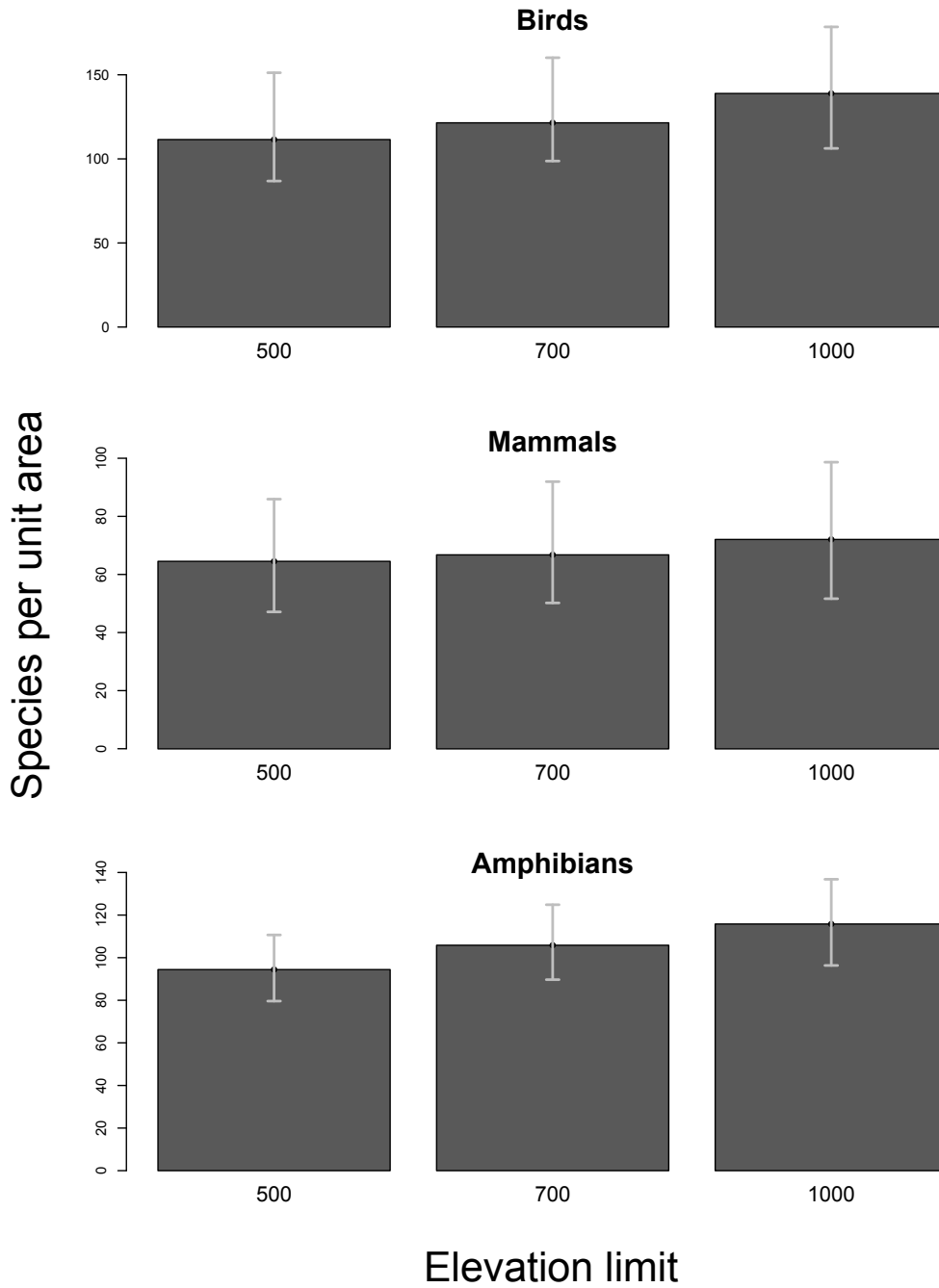
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460 **Fig. S7.** Geographical distribution of discrepant pixels between the two mountain definitions (Elevation-700 m and  
461 Ruggedness). Red pixels represent areas defined as mountains based on the Ruggedness raster layer, but not by the  
462 Elevation-700 raster layer. On the contrary, green pixels are these defined as mountains using the Elevation-700 raster  
463 layer, but not by the Ruggedness raster layer. The majority of discrepant pixels are located in middle elevations, between  
464 500 and 2000 meters of elevation.

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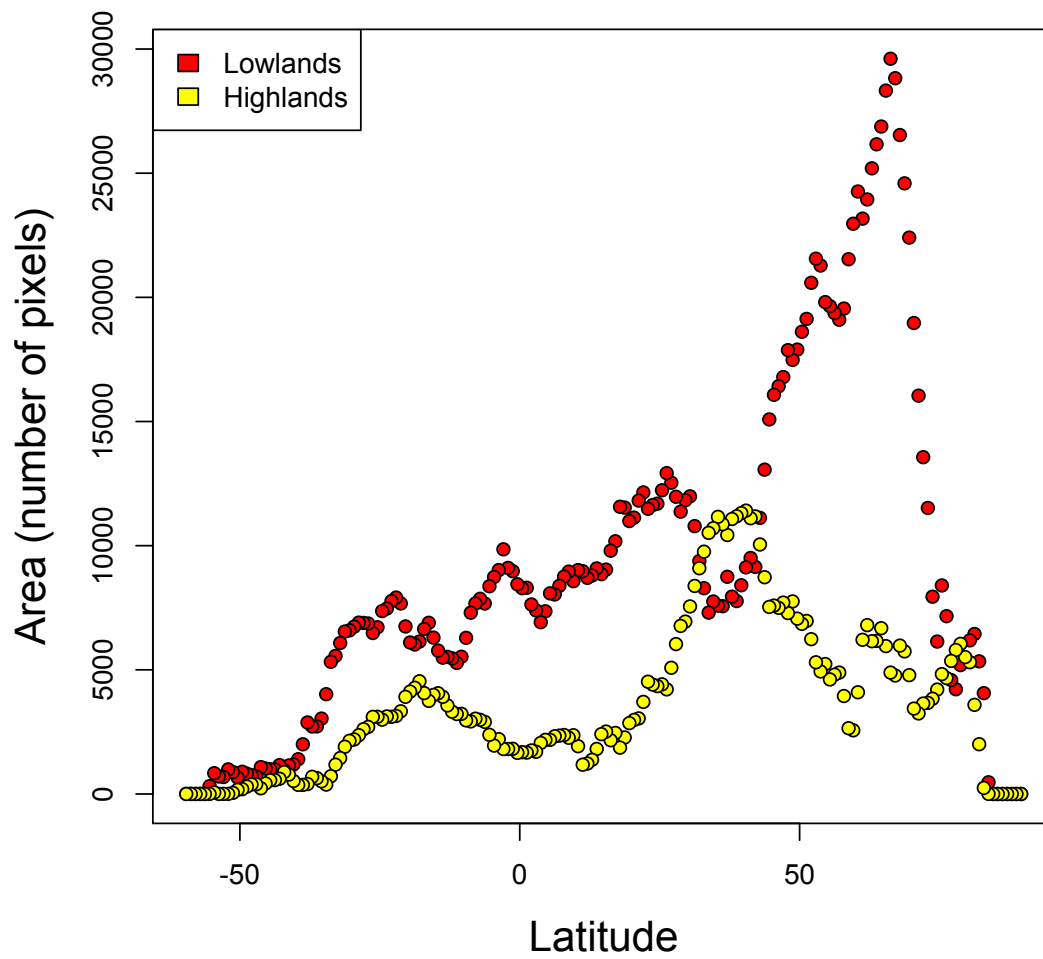
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469 **Fig. S8.** Bar plot of estimates of species per unit area for mountains using different elevation limits. Bar height  
470 corresponds to estimations using a  $T=0.5$  and intervals correspond to values generated varying  $T$  ( $T= 0.5\pm 0.2\%$ ,  $T=0.7\%$   
471 and  $T= 0.3\%$ ). Similar estimates are observed among the three elevation limits.

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474 **Fig. S9.** Estimation of area per latitudinal bands of  $0.5^\circ$  in mountains (yellow points) and lowlands (red points) as a  
475 function of latitude.

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478 **Table S1.** Estimation of mountain and lowland contribution to the total species richness of terrestrial vertebrates (global  
 479 diversity). Values are given for different thresholds ( $T$ ) for defining a mountain species ( $0.5 \pm 0.2\%$ ), and based on a  
 480 ruggedness-based mountain definition. Reported are the number of species in mountains and lowlands and the respective  
 481 percentage is given in brackets.

Group	Proportion of mountain distribution ( $T$ )	Mountain species	Lowland species	Mountain species per unit area	Lowland species per unit area
All groups	0.3	11541 (53%)	10195 (47%)	641.17	124.33
	0.5	8483 (39%)	13253 (61%)	471.28	161.62
	0.7	5848 (27%)	15888 (73%)	324.89	193.76
Birds	0.3	5066 (50%)	5118 (50%)	281.44	62.41
	0.5	3516 (35%)	6668 (65%)	195.33	81.32
	0.7	2331 (23%)	7853 (77%)	129.50	95.77
Amphibians	0.3	3797 (61%)	2467 (39%)	210.94	30.09
	0.5	3121 (50%)	3143 (50%)	173.39	38.33
	0.7	2391 (38%)	3873 (62%)	132.83	47.23
Mammals	0.3	2678 (51%)	2610 (49%)	148.78	31.83
	0.5	1846 (35%)	3442 (65%)	102.56	41.98
	0.7	1126 (21%)	4162 (79%)	62.56	50.76

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486 **Table S2.** Mean value and 95% confidence interval (in brackets) of the coefficient of determination ( $R^2$ ) and the slope ( $\beta$ )  
487 of the linear model predicting species richness against latitude for mountains and lowlands using the elevation-based  
488 definition of mountains.

	Coefficient of determination ( $R^2$ )		Slope ( $\beta$ )	
	Mountains	Lowlands	Mountains	Lowlands
All groups	0.51 (0.47, 0.56)	0.24 (0.18, 0.30)	-0.0041 (-0.0044, -0.0038)	-0.0026 (-0.0029, -0.0023)
Birds	0.44, (0.38, 0.50)	0.20 (0.15, 0.26)	-0.0041 (-0.0044, -0.0037)	-0.0025 (-0.0028, -0.0022)
Amphibians	0.46 (0.42, 0.50)	0.39 (0.35, 0.44)	-0.0041 (-0.0043, -0.0039)	-0.0038 (-0.0040, -0.0035)
Mammals	0.56 (0.51, 0.60)	0.23 (0.17, 0.29)	-0.0035 (-0.0037, -0.0033)	-0.0023 (-0.0025, -0.0020)

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492 **Table S3.** Mean value and 95% confidence interval (in brackets) of the coefficient of determination ( $R^2$ ) and the slope ( $\beta$ )  
493 of the linear model predicting species richness against latitude for mountains and lowlands using the ruggedness-based  
494 definition of mountains.

	Coefficient of determination ( $R^2$ )		Slope ( $\beta$ )	
	Mountains	Lowlands	Mountains	Lowlands
All groups	0.58 (0.52, 0.64)	0.48 (0.43, 0.54)	-0.0038 (-0.0040, -0.0036)	-0.0041 (-0.0043, -0.0039)
Birds	0.68 (0.63, 0.72)	0.56 (0.51, 0.61)	-0.0049 (-0.0052, -0.0047)	-0.0052 (-0.0054, -0.0049)
Amphibians	0.47 (0.43, 0.52)	0.46 (0.41, 0.50)	-0.0039 (-0.0041, -0.0037)	-0.0041 (-0.0044, -0.0039)
Mammals	0.34 (0.27, 0.41)	0.29 (0.23, 0.36)	-0.0025 (-0.0027, -0.0022)	-0.0026 (-0.0028, -0.0023)

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