

1 **Evolutionary dynamics of the elevational diversity gradient in passerine birds**

2

3 Paul van Els^{1,2*}, Leonel Herrera-Alsina^{1,3*\$}, Alex L. Pigot⁴⁺, and Rampal S. Etienne¹⁺

4

5 1. Groningen Institute for Evolutionary Life Sciences, University of Groningen, Box
6 11103, 9700 CC Groningen, The Netherlands.

7 2. Sovon Dutch Centre for Field Ornithology, 6525 ED Nijmegen, The Netherlands
8 (current address).

9 3. School of Biological Sciences, University of Aberdeen, AB24 2TZ, Aberdeen, UK
10 (current address).

11 4. Centre for Biodiversity and Environment Research, Department of Genetics,
12 Evolution and Environment, University College London, London, UK.

13

14 * These authors contributed equally.

15 + These authors jointly supervised this work.

16 \$ Corresponding author: leonelhalsina@gmail.com

17

18

19 **ABSTRACT**

20 Low elevation regions harbor the majority of the world's species diversity compared to
21 high elevation areas. This global gradient suggests that lowland species have had
22 more time to diversify, or that net diversification rates have been higher in the lowlands.
23 However, highlands seem to be cradles of diversity as they contain many young
24 endemics, suggesting that their rates of speciation are exceptionally fast. Here, we
25 use a phylogenetic diversification model that accounts for the dispersal of species
26 between different elevations to examine the evolutionary dynamics of the elevational
27 diversity gradient in passerine birds, a group that has radiated globally to occupy
28 almost all elevations and latitudes. We find strong support for a model where
29 passerines diversify at the same rate in the highlands and the lowlands but where the
30 per capita rate of dispersal from high to low elevations is more than twice as fast as in
31 the reverse direction. This suggests that while there is no consistent trend in
32 diversification across elevations, part of the diversity generated by highland regions
33 migrates into the lowlands, thus setting up the observed gradient in passerine
34 diversity. We find that this process drives tropical regions but for temperate areas, the
35 analysis could be hampered by their lower richness. Despite their lower diversity,
36 highland regions are disproportionately important for maintaining diversity in the
37 adjacent lowlands

38 **Keywords:** lineage dispersal; diversification rates; species elevation distributions;
39 species pump

40

41 The striking differences in the form and diversity of life as one travels up mountains is
42 one of the most prominent and long recognized patterns in biogeography ¹. Across
43 animals and plants, and across mountains globally, diversity tends to peak at low or
44 intermediate elevations and then declines towards mountain summits ^{2,3}. Thus, while
45 mountain regions are global hotspots of diversity ^{4,5}, most species occur in the
46 lowlands with relatively few species in the highlands. One possible explanation for this
47 global elevational diversity gradient (EDG) is that for most organism groups, there has
48 been more time for species to accumulate at low to intermediate elevations, with
49 highland environments only colonized more recently ⁶. Another, but not mutually
50 exclusive, possibility is that net rates of diversification are faster in the lowlands,
51 because the greater area or energy availability increases the ecological limit to
52 diversity or promotes faster intrinsic rates of speciation and lower extinction ⁷. Yet,
53 there is also evidence that highland regions may be cradles of species diversity,
54 characterized by exceptionally fast rates of speciation ^{8,9}. In other words, speciation
55 may be fastest at high elevations, even though species diversity is currently lowest
56 there ³. This suggests a third possible factor contributing to the EDG: species
57 generated in disproportionately larger numbers in the highlands migrate to the lowlands.

58 Macroecological studies of current species distribution patterns have long
59 supported the idea that highlands may be hotbeds of evolution, especially in the tropics
60 ¹⁰. Large numbers of endemic species are concentrated on tropical mountains, far
61 more than would be expected by chance or current climate ¹¹. More recent
62 phylogenetic studies have shown that many of these endemic species are
63 comparatively young, pointing towards rapid speciation ^{12,13}. There are various
64 reasons why rates of speciation may be faster at high elevations, including the
65 fragmentation of habitats on different mountain summits ¹³, ecological opportunity as

66 new habitats were made available during recent mountain uplift ¹⁴, exposure to higher
67 levels of ultraviolet radiation boosting rates of mutation ¹⁵, and the susceptibility of
68 species inhabiting narrow thermal bands to become isolated by the expansion of
69 glaciers during recurring ice ages ^{12,16}. All these factors are thought to be particularly
70 important in the tropics because limited seasonal variation enables the greater thermal
71 stratification of species across mountain slopes, enhancing opportunities for
72 geographic isolation and divergent ecological selection ¹⁷. However, while some
73 studies have supported the idea that diversification is faster in the highlands ¹⁸, others
74 studies have found no evidence for differences in diversification rates across
75 elevations ¹⁹, and thus whether rates of diversification vary consistently across
76 elevation remains debated.

77 One explanation for this lack of resolution is that the dynamics of the EDG may
78 be highly variable, differing between mountain regions with contrasting geological
79 histories and geographic properties ²⁰. For instance, some highland lineages in the
80 Andes have undergone explosive radiations, but such cases appear to be less
81 common in mountain systems in the Afrotropics ²⁰. In addition, gradients in diversity
82 — as well the phylogenetic branching times used to model these gradients — arise
83 not only from differences in diversification but also the dispersal of lineages across
84 elevations. Yet, models accounting for both differences in diversification as well as the
85 movement of species between elevational bands have rarely been applied. Some
86 verbal models predict that highland communities are evolutionary sinks, derived
87 primarily from the lowland taxa either invading or being passively transported to higher
88 elevations during mountain uplift ²¹. Other verbal models predict that highland regions
89 act as species pumps, with lineages arising at higher elevations moving downslope ^{21–}
90 ²⁵, providing an important contributor to the greater diversity of the adjacent lowlands,

91 and leading to high species richness at the ecotone between mountains and lowlands,
92 particularly in the tropics^{2,3}. Given this complexity, establishing the evolutionary
93 dynamics of the EDG requires developing empirically testable models that integrate
94 the processes of diversification and dispersal while also accounting for potential
95 differences in diversification dynamics across species, latitudes and regions.

96 Here, we study the dynamics of the EDG of passerine birds, a global ‘super
97 radiation’ of exceptional diversity, including approximately 5700 species, found at
98 almost all elevations, latitudes and biogeographic realms (other than Antarctica).
99 Passerines have arisen in approximately the last 47 million years²⁶, and represent an
100 ideal study group. Passerines show a clear EDG, with over 8 times as many species
101 present in the lowlands (n = 5095, lower elevation bound < 1500 m) as there are mid
102 (> 1500 m) or high (> 3000 m) elevation specialists combined (n = 611) (**Figure 1**;
103 **Supplementary Table 1**). The sheer diversity of passerines, combined with the
104 availability of phylogenetic trees²⁷, provides substantial power for comparing
105 competing scenarios of diversification and dispersal between different elevation bands
106 (**Figure 1**). Importantly, although characterizing the distribution of species in
107 topographically diverse regions is challenging, the elevational ranges of passerines
108 are relatively well known, with estimates of upper and lower elevation limits available
109 for almost all (96%) species.

110 Using this dataset, we first examine the relationship across passerines between
111 the elevational state of a species and its tip-DR metric, which reflects speciation rate
112²⁸ and has previously been applied to test for latitudinal and elevation gradients in
113 avian evolutionary rates³. Because this metric does not account for the movement of
114 species between elevational bands, we then apply a recently developed dynamic
115 phylogenetic model (SecSSE,²⁹), that in addition to testing for elevation-dependent

116 rates of speciation and extinction, also enables us to account for the transition of
117 species between different elevational states over evolutionary time. Using this
118 dynamic model, we are also able to test whether species movement downhill is faster
119 or slower than the rate of movement uphill, and thus whether highlands act a source
120 or sink of species diversity respectively. Finally, because there is evidence that rates
121 of diversification in passerines may vary between the tropics and temperate zone ³⁰
122 and between the New and Old World ²⁷ we allow rates of speciation (or extinction) to
123 vary either between different longitudinal (Old and New World) or latitudinal (tropics
124 and temperate) regions, when testing for an effect of elevation (**Figure 2**).

125 **RESULTS**

126 **Diversification and dispersal across elevations**

127 When comparing the tip-DR of species currently occurring in the lowlands and the
128 highlands, rates of speciation are inferred to be slightly but significantly faster in the
129 highlands. This is consistent with previous assemblage-level analyses, indicating that
130 the average tip-DR of highland bird assemblages is greater than that of lowland bird
131 assemblages ³. However, closely related species show a strong tendency to share
132 similar tip-DR values (Pagel's $\lambda = 0.987$, 95% CI: 0.984-0.99), and thus any
133 association between elevation and speciation rate could be driven by phylogenetic
134 non-independence. In accordance with this, when shared ancestry is accounted for
135 with a phylogenetic generalized linear model (PGLS), the relationship between
136 elevation and tip-DR disappears (**Supplementary Table 2**).

137 While this result suggests that there is no association between elevation and
138 speciate rate, this analysis must be interpreted with caution because it assumes that
139 species distributions are static and thus does not account for the movement of species

140 between different elevational bands over evolutionary time. To address this
141 shortcoming, we next fitted a dynamic model that estimates the diversification rate
142 associated with each elevation state as well as the transition rates between these
143 states. We compared the fit of a model in which rates of speciation (or extinction) vary
144 across elevation to two alternative null models. First, a constant rate model, in which
145 all lineages share an identical rate of diversification. Second, a concealed-trait
146 dependent model, in which rates of diversification are allowed to vary across lineages
147 due to another 'hidden' trait, but they do so independently of elevation. This second
148 null model is more realistic because it accounts for the possibility that rates of
149 diversification have been heterogeneous across passerines, and means that support
150 for elevation-dependent rates of diversification does not arise simply because of the
151 unrealistic assumption of a constant rate of diversification across such a large clade.

152 When compared to a standard constant rate (CR) null model, in which rates of
153 diversification are equal across elevational states, an Elevation-dependent (ED)
154 model, in which rates of diversification increase with elevation, is more strongly
155 supported. This result seemingly supports previous analyses suggesting faster rates
156 of bird diversification in the highlands³. However, when compared to a concealed trait-
157 dependent (CTD) null model, in which rates of diversification are allowed to vary
158 across lineages but independently of elevation, the CTD null model is overwhelmingly
159 supported (AICw ~ 0.99). Thus, while our results provide substantial support for a
160 scenario in which diversification rates vary across lineages, this variation is likely due
161 to other factors than elevation (**Supplementary Table 3**). The best supported model
162 is a latitudinal-CTD model, in which rates of speciation are 1.4 times faster in the
163 tropics than the temperate zone. Across all models, extinction is estimated to be low
164 (latitudinal-CTD model, $\mu = 0.0001/\text{myr}$) and a latitudinal-CTD model with

165 heterogeneity in rates of speciation, is more strongly supported than a CTD model with
166 heterogeneity in rates of extinction across lineages and/or regions. Finally, we find no
167 evidence for differences in rates of diversification between the Old and New World
168 **(Supplementary Table 3)**.

169 While we find no effect of elevation on rates of diversification, we find
170 substantial differences in rates of downhill and uphill dispersal. According to the best
171 model, the estimated per lineage rate of downhill dispersal is 0.189/myr, substantially
172 faster than the uphill dispersal rate of 0.072/myr **(Figure 2)**. This model of faster
173 downhill dispersal is much more strongly supported than an alternative expansion-
174 contraction scenario, in which rates of elevational range expansion and contraction
175 may differ, but there is no difference between uphill and downhill movement **(Figure**
176 **2)**. The best-supported model allows transition rates between elevational states to
177 differ from those of the transition rates between the concealed trait states, rather than
178 assuming that these are identical **(Supplementary Table 3)**, even though the former
179 model has more parameters. We find, as may be expected, that lineages disperse
180 between continents at rates that are smaller than dispersal across elevational bands.
181 The best model shows that the rate of lineage exchange between the tropics and
182 temperate zone is 0.0187/myr with lineage dispersal between the Old World and New
183 World occurring at a rate of 0.00016/myr **(Figure 2)**. Note that all these rates are per-
184 lineage rates.

185 Most passerines are tropical and so to test whether our results hold when using
186 a tropical subgroup, we repeated our analysis focusing on the ovenbirds, a large
187 tropical radiation ($n = 285$ species). Ovenbirds are spread across latitudinal bands in
188 similar proportion as the entire dataset, they inhabit only the New World tropical region,
189 and a high quality and comprehensively sampled phylogenetic tree is available³¹. The

190 results for ovenbirds are consistent with those from the global analysis, with no
191 evidence of differences in diversification across elevation, and the Uphill-Downhill
192 model receiving the highest support, with the rate of downhill dispersal (0.3176)
193 substantially exceeding the rate of uphill dispersal (0.1538).

194 Species whose modern distribution suggests limited access to mountain ranges
195 first have to expand their range in the lowlands before being able to move to a higher
196 elevation. To test whether these species influence the inferred differences in rates of
197 uphill and downhill dispersal, we added an additional state (L-) to our model. The L-
198 was assigned to lineages without direct access to mid- and high-montane areas
199 anywhere in their range or abutting their range (i.e., either island endemics or species
200 with a localized lowland distribution; $n = 146$). Even after accounting for these species,
201 our conclusions remained unchanged (**Supplementary Table 4**), with no evidence for
202 differential diversification across elevation but strong support for faster downhill than
203 uphill dispersal.

204

205 **Geographic origin of passerines and accumulation of lineages over time**

206 Because the elevational origin of passerines can have an important influence on the
207 current gradient of species richness, we extracted the probabilities (using the best
208 supported model) of each state (i.e., the combination of elevation and latitude) at the
209 most-basal node of the phylogeny to estimate where the clade first appeared. These
210 probabilities indicate the most likely state of the ancestral species just before it splits
211 at the crown of the phylogeny, and so the true origin of the clade (at the stem age)
212 may have been different. Regardless of whether rates of diversification are allowed to
213 vary with latitude or longitudinal region, a highland origin of passerines is equally well

214 supported as a lowland origin. This lack of strong support for either elevational state
215 reflects the relatively rapid transitions across elevation inferred by our analysis and
216 which have likely erased this historical signal of where passerines originated.

217 **DISCUSSION**

218 In spite of clear differences in passerine diversity at different elevations, we find no
219 difference in diversification rates across elevational zones. Instead, the best supported
220 scenario is a Latitudinal-Concealed-Trait Dependent model with higher per capita
221 rates of downhill dispersal than uphill dispersal. This CTD model indicates that there
222 is substantial variation in diversification rates across lineages and latitude, but that this
223 variation is not related to elevation. Thus, while previous more taxonomically or
224 geographically focused studies have found evidence for differences in diversification
225 across elevation, this is not supported by our global analysis across all passerines.

226 The absence of a consistent effect of elevation on diversification is unlikely to
227 be explained by a lack of statistical power. Our analysis contains thousands of species
228 and our model did detect faster rates of diversification in the tropics compared to the
229 temperate zone. This suggests that if there was a globally coherent effect of elevation
230 on diversification, this would also have been detected in our analysis. Furthermore,
231 the absence of any effect of elevation on diversification cannot be explained by a
232 failure of our model to detect finer-scale heterogeneity in diversification rates within
233 the tropics or temperate zone. The strong support for the Concealed Trait-Dependent
234 model confirms that there is indeed substantial heterogeneity in rates of diversification
235 across passerines within these regions, but that this variation is not aligned with
236 elevation. Critically, our results show that failure to account for this background
237 heterogeneity in rates of diversification would have led to the spurious conclusion that

238 rates of diversification do increase with elevation. We therefore suggest that
239 application of such a Concealed Trait-Dependent model is an important advance that
240 should also be applied when examining other putative drivers of diversification rates
241 (e.g., body size).

242 One possible explanation for why our global analysis does not detect an
243 elevational gradient in diversification, is that different dynamics may prevail in different
244 regions obscuring the overall importance of elevation. Differences across latitude may
245 be particularly important in this regard, because it is mainly highlands in the tropics
246 where rates of speciation are thought to be promoted ³². However, this is unlikely to
247 explain our results because most of the species in our analysis (85%) occur in the
248 tropics, and thus it is the dynamics of the EDG in this region which dominate our model
249 inferences. Indeed, our results based on the tropical ovenbirds are highly consistent
250 with the general pattern. Rather, our results suggest that net rates of diversification
251 are boosted in the tropics, but this occurs regardless of elevation.

252 Another possibility is that although diversification and elevation may be related
253 in some mountain systems, these effects of elevation are highly context dependent,
254 determined by the particular geological history and environment in different mountains
255 ³. Accounting for such variability is challenging because it would require a substantial
256 increase in model complexity and the number of parameters that need to be inferred.
257 We note that support for such a complex model would not alter our main conclusion
258 that, at a global scale, there is no consistent trend in diversification across elevation.

259 Our finding that net rates of diversification in passerines do not vary consistently
260 with elevation contrasts with that of a recent study showing that diversification rates
261 increase with elevation ³. We note a number of important methodological differences

262 that may explain these contrasting findings. Quintero and Jetz (2018) calculated
263 speciation rate for each extant passerine species (tip-DR) and then averaged this
264 across all the species inhabiting each elevational band across major mountain
265 systems. This approach strongly differs from ours, because it mainly captures recent
266 speciation and because it links the speciation rate of a lineage to its current elevation.
267 This approach ignores dispersal across elevational bands and thus the possibility that
268 the speciation events leading to a particular lineage occurred at a different elevation
269 to where that species currently resides. Furthermore, while the shared phylogenetic
270 history of each species is automatically accommodated in our dynamic model (i.e.,
271 each branch of the tree is only counted once), our results show that treating each
272 species as statistically independent when analyzing tip-DR may lead to spurious
273 results. On the basis of these results, we suggest that accounting for the
274 biogeographic dynamics and phylogenetic non-independence of lineages is likely to
275 be critical when making inferences of how rates of diversification vary across elevation
276 or any other gradient.

277 Much of the research on the evolutionary dynamics of the EDG has focused on
278 explaining patterns at relatively fine taxonomic scales or particular mountain systems.
279 While these have provided evidence for both uphill ³³ and downhill ³⁴ movement of
280 species, they have often supported the idea that most clades originated in the lowlands
281 and then invaded higher elevations ³⁵. For example among avian genera, *Leptopogon*
282 flycatchers ²³, Chat-tyrants ²⁵, *Andropadus* greenbuls ²⁴ and *Thamnophilus* antshrikes
283 ³⁶ show a repeated movement of species into the highlands followed by in situ
284 diversification. Larger and older clades, however, paint a more complex picture, with
285 McGuire et al (2007) providing evidence that hummingbirds (Trochilidae) have
286 undergone multiple colonizations of Andes from the lowlands, but also the reverse.

287 Our findings across passerines, place these previous genus- and family-level studies
288 in a broader context, showing that while there are many cases of uphill dispersal
289 followed by radiation, overall, on a per-lineage basis, the dispersal from high to low
290 elevations, occurs at a much faster rate.

291 Why per-lineage rates of dispersal from highlands to lowlands are faster than
292 the reverse remains unclear. Indeed, most studies have suggested a net movement
293 of species uphill, either because of ecological opportunity ¹⁴ or passive transportation
294 during mountain uplift ²¹. A non-biological explanation of higher rates of dispersal
295 downhill than uphill could be that available area decreases with elevation, which allows
296 more species to fit in the lowlands. Another possible mechanism is that strong
297 physiological limitations prevent adaptation to higher elevations (i.e., UV-radiation and
298 oxygen availability vary across altitude). For instance, bird species living at high
299 altitude show a loss of genes related to immune response and require a specific
300 machinery to repair cellular damage caused by UV radiation ³⁷. Lineages adapting to
301 highlands and losing immune function might be unlikely to regain it. However, the
302 return to lowlands or the adaptation to lowlands by highland-originated lineages could
303 be mediated by the stronger expression of immune response boosted by high levels
304 of oxygen ³⁸. Additionally, decreased oxygen concentration can severely increase the
305 chances of hypoxia during flight ³⁹. Although phenotypic plasticity could partially tackle
306 this limitation ⁴⁰, evolutionary adaptations involving changes in hemoglobin affinity to
307 oxygen may be difficult to develop as there are few molecular pathways that are not
308 associated with reduced fitness i.e., deleterious pleiotropic effects ⁴¹. Furthermore,
309 species adapted to low concentration of oxygen require large lungs that are costly to
310 maintain so the switch to a lowland region might be beneficial from an energetic
311 standpoint ⁴². It is important to note that we are reporting the rates of successful

312 dispersal events between elevational bands and that dispersal events not leading to
313 establishment are not recorded. Hence, another alternative is that high elevation
314 habitats may be less conducive to colonization over macro-evolutionary timescales ⁴³
315 due to ecological constraints i.e., a lower availability of resources ⁷. In other words, it
316 is possible that lineages are equally likely to disperse regardless of the elevation they
317 arise from, but those elevational bands where the niche space is wider, are more likely
318 to accommodate colonizers. Thus, our results are potentially consistent with the idea
319 that higher ecological limits to coexistence in the lowlands ultimately underlie the EDG
320 in passerine birds ⁴⁴.

321 Our results provide support that highland regions have acted as a species pump
322 for passerine birds, not because of faster total rates of diversification, but because
323 species arising in the highlands disperse downhill. Thus while highlands constitute
324 only a fraction of passerine diversity they play a disproportionate role in boosting the
325 diversity of the lowlands. Highland species are at particular risk of extinction from
326 anthropogenic warming this century due to a lack of available cooler habitats to which
327 species can disperse ⁴⁵. Our results suggest that the loss of highland lineages will also
328 have long term impacts on the diversity of the lowlands and passerines globally.

329

330

331 **REFERENCES**

332

333

- 334 1. Lomolino, M. v. Elevation gradients of species-density: historical and prospective views.
335 *Global Ecology & Biogeography* **10**, 3–13 (2001).
- 336 2. McCain, C. M. Global analysis of reptile elevational diversity. *Global Ecology and*
337 *Biogeography* **19**, 541–553 (2010).
- 338 3. Quintero, I. & Jetz, W. Global elevational diversity and diversification of birds. *Nature* **555**,
339 246–250 (2018).
- 340 4. Orme, C. D. L. *et al.* Global hotspots of species richness are not congruent with endemism or
341 threat. *Nature* **436**, 1016–1019 (2005).
- 342 5. Rahbek, C. *et al.* Humboldt’s enigma: What causes global patterns of mountain biodiversity?
343 *Science* **365**, 1108–1113 (2019).
- 344 6. Wiens, J. J., Parra-Olea, G., García-París, M. & Wake, D. B. Phylogenetic history underlies
345 elevational biodiversity patterns in tropical salamanders. *Proceedings of the Royal Society B:*
346 *Biological Sciences* **274**, 919–928 (2007).
- 347 7. Pigot, A. L., Trisos, C. H. & Tobias, J. A. Functional traits reveal the expansion and packing of
348 ecological niche space underlying an elevational diversity gradient in passerine birds.
349 *Proceedings of the Royal Society B: Biological Sciences* **283**, 1–9 (2016).
- 350 8. Körner, C. & Spehn, E. M. *Mountain biodiversity: a global assesment.* (2002).
- 351 9. Merckx, V. S. F. T. *et al.* Evolution of endemism on a young tropical mountain. *Nature* **524**,
352 347–350 (2015).
- 353 10. Fjeldsa, J. Geographical patterns for relict and young species of birds in Africa and South
354 America and implications for conservation priorities. *Biodiversity and Conservation* **3**, 207–
355 226 (1994).
- 356 11. Jetz, W., Rahbek, C. & Colwell, R. K. The coincidence of rarity and richness and the potential
357 signature of history in centres of endemism. *Ecology Letters* **7**, 1180–1191 (2004).
- 358 12. Weir, J. T. Divergent timing and patterns of species accumulation in lowland and highland
359 neotropical birds. *Evolution* **60**, 842–855 (2006).
- 360 13. Hughes, C. & Eastwood, R. Island radiation on a continental scale: Exceptional rates of plant
361 diversification after uplift of the Andes. *Proceedings of the National Academy of Sciences of*
362 *the United States of America* **103**, 10334–10339 (2006).
- 363 14. Cozzarolo, C. S. *et al.* Biogeography and ecological diversification of a mayfly clade in New
364 Guinea. *Frontiers in Ecology and Evolution* **7**, (2019).

- 365 15. Davies, T. J., Savolainen, V., Chase, M. W., Moat, J. & Barraclough, T. G. Environmental energy
366 and evolutionary rates in flowering plants. *Proceedings of the Royal Society B: Biological*
367 *Sciences* **271**, 2195–2200 (2004).
- 368 16. Graves, G. R. Linearity of geographic range and its possible effect on the population structure
369 of andean birds. *The Auk* **105**, 47–52 (1988).
- 370 17. Janzen, D. H. Why mountain passes are higher in the tropics. *The American Naturalist* **101**,
371 233–249 (1967).
- 372 18. Cai, T. *et al.* What makes the Sino-Himalayan mountains the major diversity hotspots for
373 pheasants? *Journal of Biogeography* **45**, 640–651 (2018).
- 374 19. Rana, S. K., Gross, K. & Price, T. D. Drivers of elevational richness peaks, evaluated for trees in
375 the east Himalaya. *Ecology* **100**, (2019).
- 376 20. Rahbek, C. *et al.* Building mountain biodiversity: Geological and evolutionary processes.
377 *Science* **365**, 1114–1119 (2019).
- 378 21. Ribas, C. C., Moyle, R. G., Miyaki, C. Y. & Cracraft, J. The assembly of montane biotas: Linking
379 Andean tectonics and climatic oscillations to independent regimes of diversification in Pionus
380 parrots. *Proceedings of the Royal Society B: Biological Sciences* **274**, 2399–2408 (2007).
- 381 22. Schwery, O. *et al.* As old as the mountains: The radiations of the Ericaceae. *New Phytologist*
382 **207**, 355–367 (2015).
- 383 23. Bates, J. M. & Zink, R. M. Evolution into the Andes: Molecular Evidence for Species
384 Relationships in the Genus *Leptopogon*. *The Auk* **111**, 507–515 (1994).
- 385 24. Roy, M. S. Recent diversification in African greenbuls (Pycnonotidae: *Andropadus*) supports a
386 montane speciation model. *Proceedings of the Royal Society B: Biological Sciences* **264**, 1337–
387 1344 (1997).
- 388 25. Garcia-Moreno, J. *et al.* Pre-pleistocene differentiation among chat-tyrarants. *The Condor*
389 **100**, 629–640 (1998).
- 390 26. Oliveros, C. H. *et al.* Earth history and the passerine superradiation. *Proceedings of the*
391 *National Academy of Sciences of the United States of America* **116**, 7916–7925 (2019).
- 392 27. Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Mooers, A. O. The global diversity of birds in
393 space and time. *Nature* **491**, 444–448 (2012).
- 394 28. Title, P. O. & Rabosky, D. L. Tip rates, phylogenies and diversification: What are we
395 estimating, and how good are the estimates? *Methods in Ecology and Evolution* **10**, 821–834
396 (2019).
- 397 29. Herrera-Alsina, L., van Els, P. & Etienne, R. S. Detecting the Dependence of Diversification on
398 Multiple Traits from Phylogenetic Trees and Trait Data. *Systematic Biology* **68**, (2019).
- 399 30. Weir, J. T. & Schluter, D. The latitudinal gradient in recent speciation and extinction rates of
400 birds and mammals. *Science* **315**, 1574–1576 (2007).
- 401 31. Derryberry, E. P. *et al.* LINEAGE DIVERSIFICATION AND MORPHOLOGICAL EVOLUTION IN A
402 LARGE-SCALE CONTINENTAL RADIATION: THE NEOTROPICAL OVENBIRDS AND
403 WOODCREEPERS (AVES: FURNARIIDAE). *Evolution* **65**, 2973–2986 (2011).

- 404 32. Fjeldså, J., Bowie, R. C. K. & Rahbek, C. The Role of Mountain Ranges in the Diversification of
405 Birds. *Annual Review of Ecology, Evolution, and Systematics* **43**, 249–265 (2012).
- 406 33. Chazot, N. *et al.* Into the Andes: multiple independent colonizations drive montane diversity
407 in the Neotropical clearwing butterflies Godyridina. *Molecular Ecology* **25**, 5765–5784 (2016).
- 408 34. Elias, M. *et al.* Out of the Andes: Patterns of diversification in clearwing butterflies. *Molecular*
409 *Ecology* **18**, 1716–1729 (2009).
- 410 35. McGuire, J. A., Witt, C. C., Altshuler, D. L. & Remsen, J. v. Phylogenetic systematics and
411 biogeography of hummingbirds: Bayesian and maximum likelihood analyses of partitioned
412 data and selection of an appropriate partitioning strategy. *Systematic Biology* **56**, 837–856
413 (2007).
- 414 36. Brumfield, R. T. & Edwards, S. v. Evolution into and out of the Andes: A Bayesian analysis of
415 historical diversification in *Thamnophilus antshrikes*. *Evolution* **61**, 346–367 (2007).
- 416 37. Zhou, C. *et al.* Genome-wide analysis sheds light on the high-altitude adaptation of the buff-
417 throated partridge (*Tetraophasis szechenyii*). *Molecular Genetics and Genomics* **295**, 31–46
418 (2020).
- 419 38. Xu, Z., He, J. & Wang, J. Hypoxia affects the resistance of *Scylla paramamosain* to *Vibrio*
420 *alginolyticus* via changes of energy metabolism. *Aquaculture Reports* **19**, 100565 (2021).
- 421 39. Storz, J. F., Scott, G. R. & Cheviron, Z. A. Phenotypic plasticity and genetic adaptation to high-
422 altitude hypoxia in vertebrates. *Journal of Experimental Biology* vol. 213 4125–4136 (2010).
- 423 40. Scott, G. R. Elevated performance: The unique physiology of birds that fly at high altitudes.
424 *Journal of Experimental Biology* vol. 214 2455–2462 (2011).
- 425 41. Projecto-Garcia, J. *et al.* Repeated elevational transitions in hemoglobin function during the
426 evolution of Andean hummingbirds. *Proceedings of the National Academy of Sciences of the*
427 *United States of America* **110**, 20669–20674 (2013).
- 428 42. Scott, G. R. *et al.* Molecular evolution of cytochrome c oxidase underlies high-altitude
429 adaptation in the bar-headed goose. *Molecular Biology and Evolution* **28**, 351–363 (2011).
- 430 43. Schumm, M., White, A. E., Supriya, K. & Price, T. D. Ecological limits as the driver of bird
431 species richness patterns along the east himalayan elevational gradient. *American Naturalist*
432 **195**, 802–817 (2020).
- 433 44. Etienne, R. S. *et al.* A minimal model for the latitudinal diversity gradient suggests a dominant
434 role for ecological limits. *American Naturalist* **194**, E122–E133 (2019).
- 435 45. Freeman, B. G., Scholer, M. N., Ruiz-Gutierrez, V. & Fitzpatrick, J. W. Climate change causes
436 upslope shifts and mountaintop extirpations in a tropical bird community. *Proceedings of the*
437 *National Academy of Sciences of the United States of America* **115**, 11982–11987 (2018).
- 438 46. Bouckaert, R. *et al.* BEAST 2: A Software Platform for Bayesian Evolutionary Analysis. *PLoS*
439 *Computational Biology* **10**, (2014).
- 440 47. Braun, E. L., Cracraft, J. , & Houde, P. Resolving the avian tree of life from top to bottom: The
441 promise and potential boundaries of the phylogenomic era. in *Avian Genomics in Ecology and*
442 *Evolution* 151–210 (2019).

- 443 48. del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A. & Kirwan, G. *Handbook of the Birds of the*
444 *World Alive*. (Barcelona: Lynx Edicions., 2016).
- 445 49. Chapman, F. M. The distribution of bird life in Ecuador. *Bulletin of the American Museum of*
446 *Natural History* **55**, 1–784 (1926).
- 447 50. Maddison, W. P., Midford, P. E. & Otto, S. P. Estimating a binary character’s effect on
448 speciation and extinction. *Systematic biology* **56**, 701–710 (2007).
- 449 51. Beaulieu, J. M. & O’Meara, B. C. Detecting hidden diversification shifts in models of trait-
450 dependent speciation and extinction. *Systematic Biology* **65**, 583–601 (2016).
- 451 52. Herrera-Alsina, L., van Els, P. & Etienne, R. S. Detecting the Dependence of Diversification on
452 Multiple Traits from Phylogenetic Trees and Trait Data. *Systematic Biology* **68**, 317–328
453 (2019).
- 454 53. Harmon, L. J., Weir, J. T., Brock, C. D., Glor, R. E. & Challenger, W. GEIGER: Investigating
455 evolutionary radiations. *Bioinformatics* **24**, 129–131 (2008).
- 456 54. Daru, B., Karunarathne, P. & Schliep, K. phyloregion: R package for biogeographic
457 regionalization and spatial conservation. *bioRxiv* (2020) doi:10.1101/2020.02.12.945691.
- 458

459

460

461 **ACKNOWLEDGMENTS**

462 PVE's research was facilitated by the Adaptive Life Program of the Groningen
463 Institute for Evolutionary Life Sciences, Faculty of Science and Engineering at the
464 University of Groningen. LH-A thanks the Consejo Nacional de Ciencia y Tecnologia
465 of Mexico for funding (CVU 385304 L). RSE thanks the Netherlands Organization for
466 Scientific Research (NWO) for financial support through a VICI grant. ALP is funded
467 by a Royal Society University Research Fellowship. We would like to thank the Center
468 for Information Technology of the University of Groningen for their support and for
469 providing access to the Peregrine high performance computing cluster.

470 **Author Contributions**

471 PvE collected data; LH-A and PvE performed the analysis; RSE and ALP supervised
472 the project; LH-A, PvE, ALP and RSE wrote the manuscript.

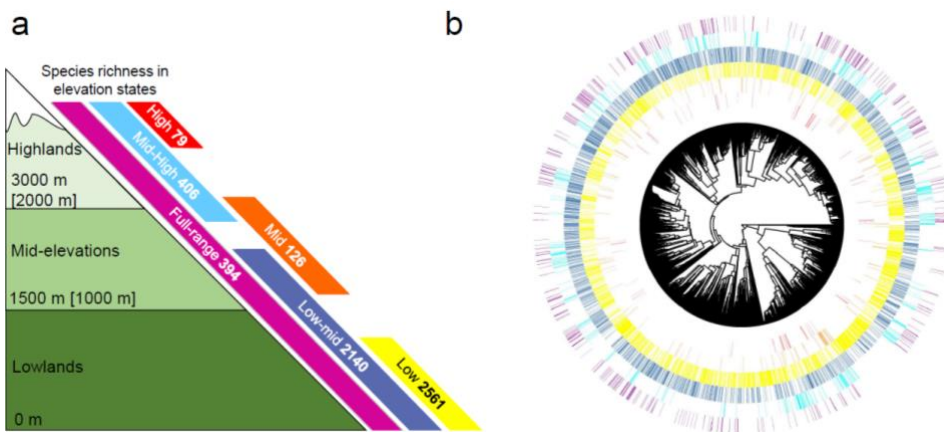
473 **Competing Interests statement**

474 The authors declare no competing interest.

475

476

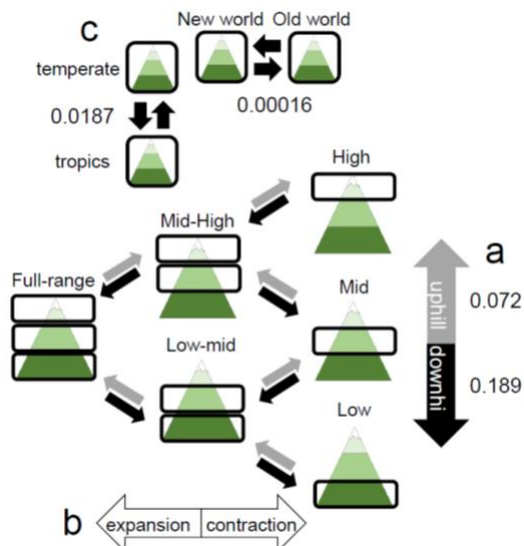
477 **FIGURES**



478

479 Figure 1. The global elevational diversity gradient (EDG) in passerine birds. a)
480 species richness in birds exhibits a decline with elevation. The three assigned
481 elevational bands (altitudinal delimitation for temperate regions is in brackets) and
482 six possible elevational states of species are shown, with the number of species in
483 each state indicated. States account for species restricted to a single elevational
484 band or that span multiple elevational bands. b) the distribution of species across
485 elevational bands within the passerine phylogenetic tree, with elevation states
486 plotted concentrically onto the phylogeny. Colors match those in 1a.

487



488

489 Figure 2. The dynamics of the EDG is modelled by allowing rates of diversification to
 490 vary across species elevational states and by allowing transitions between different
 491 elevational states over time. We model transitions between states by considering that
 492 species contract their elevational range when they become absent from an elevational
 493 band and expand their elevational range when they become present in a new
 494 elevational band. We consider two possible scenarios of how species transition
 495 between elevational states. First, in the uphill-downhill scenario (a), the rate of
 496 transition to a higher elevational state can differ from rate of transition to a lower
 497 elevational state. Second, in the expansion-contraction scenario (b), the transition to
 498 a wider elevational state (i.e. present in more elevational bands) can differ from the
 499 rate of transition to a narrower elevational state (i.e. present in fewer elevational
 500 bands). In addition to transitions between elevational states, species may also
 501 transition between either different biogeographic states, indicated either by their
 502 presence in the old or new world or the temperate or tropical zone (c). We show the
 503 per-lineage rates of transition across longitude, latitude and elevation which maximize
 504 the likelihood of the best supported model.

505

507

508 **METHODS**

509 **Phylogenetic framework**

510 We used a Bayesian pseudo-posterior distribution of time-calibrated phylogenies ²⁷,
511 which includes 9,993 of 10,473 currently recognized bird species. Using the program
512 TreeAnnotator from the BEAST2 package v2.4.2 ⁴⁶ we produced a maximum-clade
513 credibility tree from all available stage 2 trees with the Hackett backbone. We pruned
514 this tree to the level of Passeriformes ($n = 5,966$ species). We are aware of the
515 shortcomings of using a megaphylogeny that does not include sequence data for each
516 taxon ⁴⁷, but the statistical power achieved by the large number of tips and branching
517 events compensates, at least in part, for the possible lack of taxonomic precision. To
518 test if our results hold in a subset, we repeated our analysis using a phylogeny for
519 ovenbirds (Furnariidae) for which 97% of species have been sequenced ³¹.

520 **Elevation data and large-scale realms**

521 We compiled elevation data for passerines, recording lower and upper elevation
522 bounds of their distribution, based on descriptions in the Handbook of the Birds of the
523 World ⁴⁸. We did not include occasional records at extreme elevation. Elevational
524 distributions are based on the breeding range, thus excluding wintering and transient
525 elevation records. Species without known elevational distribution were assigned NA in
526 the data set ($n = 260$) rather than removed, because this could bias diversification
527 rates, and our analysis can account for this missing data (see below).

528 Our model of elevation-dependent diversification and dispersal requires
529 treating elevation as a categorical state. To do this we defined 3 elevational bands
530 whose altitudinal range vary latitudinally. In tropical regions: lowlands (from sea level

531 up to 1500 meter above sea level), mid-elevations (1500 - 3000 m), and highlands (>
532 3000 m). In temperate regions: lowlands (from 0 to 1000 m), mid-elevations (1000 -
533 2000 m), and highlands (> 2000 m). These categories broadly agree with those
534 established by ⁴⁹ for Neotropical montane birds based on the dominant vegetation
535 associated with the tropics, subtropics, and alpine zones, respectively. Species may
536 inhabit multiple bands (indeed some species span the entire elevation gradient) and
537 accounting for this variation in elevational range size is important when determining
538 the dynamics of the EDG. We therefore defined three additional categories for species
539 inhabiting more than one elevational band: low-mid, mid-high and full range (i.e.,
540 species living from lowlands to high montane areas). The number of species in each
541 category is shown in Table 1. From hereon we refer to these 6 elevational categories
542 as the elevational state of the species. While this was our main data set, we formulated
543 another data set where the lowlands category was split between lowlands adjacent to
544 mountains and lowlands that are not adjacent to mountains.

545 We first performed a global analysis in which rates of diversification depend on
546 elevation, resulting in 6 states. We then accounted for the possibility that rates of
547 diversification may differ across latitude and longitude in the following way. We
548 distinguished species occurring in the tropics from species in the temperate (latitudinal
549 analysis), so that latitude and elevation can differentially affect diversification resulting
550 in a model with 12 states (e.g., a species could be a tropical lowland species, or in a
551 temperate mid-high state). We classified species as tropical when most of the
552 latitudinal span of their breeding distribution ⁴⁸ lies between tropics of Cancer and
553 Capricorn. Finally, we distinguished Old World from New World species (longitudinal
554 analysis, again resulting in 12 possible states (e.g., Old World low-mid state), in which
555 longitude and elevation can differentially affect diversification. We did not perform an

556 analysis where diversification rates simultaneously depend on elevation, latitude and
557 longitude, because the large state space required for such an analysis was
558 computationally unfeasible and numerically unstable given the size of our phylogeny
559 (but see below).

560 **State-dependent diversification analysis and parameterization**

561 We used the SSE framework (State-dependent Speciation and Extinction) which
562 allows determining whether diversification rates are associated with an evolving trait
563 ⁵⁰. In this model, the speciation rate (λ_i) or extinction rate (μ_i) of a lineage depends on
564 its trait state i (here elevation, or a combination of elevation and latitude (tropical or
565 temperate) or longitude (New World or Old World)). In order to keep the number of
566 estimated parameters as low as possible during the likelihood optimization, we only
567 optimized the speciation (or extinction) rate of the low, mid and high elevation state
568 and used these values to obtain average rates for the states that are a combination of
569 those elevations (e.g., the low and mid elevation rates of speciation are averaged to
570 yield the rate of the low-mid elevation state).

571 The state of a species is not static, with species switching to a different state at
572 rate q_{ij} , where i and j represent the state of origin and the state of destination,
573 respectively. This allows us to use trait and branching patterns simultaneously to study
574 macroevolutionary dynamics. In other words, when lineages living in different elevation
575 states experience different speciation/extinction regimes, the shift from one elevational
576 state to another will have an effect on diversification rates. Statistical support for
577 elevation affecting diversification rates is found when the likelihood of a model where
578 speciation (or extinction; see below) differs across elevation states (Elevation-
579 Dependent model, ED) is higher — after correcting for differences in numbers of

580 parameters — than a model where rates depend on an unknown (hidden or
581 concealed) trait (Concealed Trait-Dependent, CTD) and a model with constant rates
582 (CR) ^{51,52}. The comparison in terms of likelihood between ED and CTD models is
583 important to prevent spurious conclusions regarding the association between
584 heterogeneity in diversification rates across lineages and the evolution of the trait. We
585 used the R package secsse (Several Examined and Concealed States-Dependent
586 Speciation and Extinction; ⁵²) which computes and optimizes the likelihood of the
587 model with 2 or more states.

588 We assume that species transition between elevation states via the expansion
589 into an adjacent elevation band (i.e., from low to low-mid or from high to mid-high) or
590 from contraction at the edge of the range (i.e. full range to low-mid or mid-high). In
591 other words, we do not allow disjunct elevational ranges as these are rarely observed
592 ⁷. We considered two alternative scenarios for how rates of transitions between states
593 may vary. In both cases we estimate two transition rates. First, under an Uphill-
594 Downhill model, uphill transitions have a different rate than downhill transitions. Note
595 that under the Uphill-Downhill scenario, changing from, for example, the low-mid
596 elevation state to the low elevation state means going downhill. Second, under an
597 expansion-contraction model, all expansion rates (i.e., change from one single
598 elevation band to two, or from two to three) are equal but different from contraction
599 rates (i.e., a change from two bands to a single band, or from three to two bands)
600 which are also equal. We implemented the expansion-contraction model because it
601 allows us to test a scenario where the rate at which species colonize or become extinct
602 at a particular elevation can differ, but where these rates are independent of
603 elevational direction. In other words, in contrast to the Uphill-Downhill model,
604 colonizing (or becoming extinct at) a lower or higher elevation band is equally likely.

605 As recommended by ²⁹, for the concealed trait we assumed an identical model
606 structure, in terms of the number of states and possible transitions between these. We
607 implemented two versions of the CTD model: one where the transition rates between
608 concealed states are the same as those between elevation states, and one where we
609 relax this assumption and allow the transition rates of the concealed trait to be different
610 from the transition rates between elevational bands. Because differences in
611 diversification rates across elevations could be due to either differential speciation or
612 extinction, we ran all the mentioned model combinations with two different
613 assumptions: in speciation-dependent diversification, speciation varied across states
614 while extinction remained constant. For extinction-dependent diversification, extinction
615 was free to vary across states whereas speciation was kept constant.

616 In the analysis where we added the state L⁻ that accounts for those lowland
617 species which have limited access to mountain ranges, only Lowland species could
618 expand their distribution uphill. Lineages in L⁻ need first to colonize lowlands close to
619 mountains (L) to then move to higher elevation. In this model, we allow the rates of
620 moving across elevations (or contracting/expanding) to be different from shifting from
621 L⁻ to L (and the reverse) as they are different processes. Uphill-Downhill and
622 Expansion-Contraction model structures are the same as in the global analysis. We
623 ran two versions of this model, one where the rates from L⁻ to L are different as from
624 L to L⁻ and another version where these rates are the same. The results (AICc
625 comparison; **Supplementary Table 4**) point to the former model being preferred. The
626 estimated rate to shift from L⁻ to L is 0.2865 and from L to L⁻ is 0.0106.

627 For the longitudinal and latitudinal analyses, in addition to allowing different
628 rates of diversification across elevational bands, we also allow the overall rate of
629 diversification to differ between regions (i.e. tropical vs. temperate regions, Old World

630 vs. New World). We did so by multiplying the rates in one region by a constant factor
631 to give rates in the other region and this factor was optimized. To avoid models with
632 many parameters we did not consider the more complex scenario where the elevation-
633 dependence in rates of diversification varies between regions. We assumed that the
634 transition of species between regions (region exchange) happens to and from the
635 same elevational band (low, mid and high only). While we assume that the transition
636 rates *between* regions is the same for all elevational bands, these rates are different
637 from the rates of transition between elevational bands *within* regions.

638 To prevent finding only local optima during the likelihood optimization, we used
639 five different initial parameter sets. The first set of parameters were the estimates of
640 speciation and extinction from a birth-death model fit to the branching times and with
641 transition rates assumed to be a fifth of speciation rate. For the second set, we doubled
642 the speciation rates of the first set, and halved the transition rates. In the third, we
643 halved the speciation rates of the first set and doubled the transition rates. Similarly,
644 the fourth had doubled extinction rates and halved transition rates, and the fifth had
645 halved extinction rates and doubled transition rates compared to the first set. The
646 highest likelihood of the five starting points was taken as the global optimum and used
647 to compare across models. We used AIC weights – thus penalizing the number of free
648 parameters – to select the best models per analysis.

649 Our global, latitudinal and longitudinal analyses differ in their assumptions on
650 what factors diversification rates (elevation only, elevation + latitude, elevation +
651 longitude). Using only the data necessary to study these dependencies would prevent
652 model comparison, because the data sets would differ. We had six states in the global
653 analysis (as there are six elevational bands) whereas the longitudinal analysis has 12
654 states (six bands in combination with tropical and temperate regions) which are

655 different from the 12 states in latitudinal analysis (six bands in combination with New
656 and Old worlds). Therefore, we made the AIC values comparable by adding an extra
657 likelihood term to the likelihood computed by secsse that covers the transitions not
658 covered in secsse, using the function fitDiscrete from the R package geiger⁵³. That is,
659 for the longitudinal analysis we added the (maximum) loglikelihood of a simple model
660 of transitions in latitude which uses the phylogenetic tree. In this way, the total
661 likelihood of the longitudinal analysis incorporates the likelihood of a model with
662 transitions across elevations + longitude (computed by secsse) + a model of
663 transitions between latitude (computed by geiger). Note that only the component
664 calculated using secsse handles diversification rates and state transitions
665 simultaneously. Similarly, for the latitudinal analysis we added the (maximum)
666 loglikelihood of a model of transitions in longitude given the phylogenetic tree, and for
667 the global analysis we added the (maximum) loglikelihood of a model of transitions in
668 both longitude and latitude – which in fact is the sum of the two previous loglikelihoods.

669 Finally, to provide a more direct comparison with previous studies, we also
670 examined the association between elevation and tip diversification rate (tip-DR) using
671 ANOVA and phylogenetic generalized linear model (PGLS) fitted in the R package
672 'caper'. For our predictor variable we assigned species as either 'highland' (High, Mid-
673 High) or 'lowland' (Low, Low-Mid) and excluded species limited to mid-elevations (Mid)
674 or spanning the entire gradient (Full-Range), resulting in $n = 5,186$ species. We
675 calculated tip-DR using the 'evol_distinct' function of the 'phyloregion' R package⁵⁴.

676 **Data availability**

677 No datasets were generated during the current study. Data analyzed was collected
678 from del Hoyo et al (2016): Handbook of the Birds of the World Alive and from Jetz et
679 al (2012): The global diversity of birds in space and time. Nature 491:444–448.

680 The necessary files to replicate our study are available at Figshare:
681 10.6084/m9.figshare.14750652.

682 **Code availability**

683 We used R packages for analyzing data. They are all available at CRAN: caper,
684 phyloregion, DDD and secsse. R code we used to setup models, import, and analyze
685 the output is available (Figshare: 10.6084/m9.figshare.14750652)

686

687

688

689

690

691 **TABLES**

692 **Supplementary Table 1.** Elevational distribution of passerine species richness. We
 693 defined three elevational bands: lowlands (from sea level up to 1500 meter above sea
 694 level), mid-elevations (1500-3000 m), and highlands (> 3000 m). In temperate regions:
 695 lowlands (from 0 to 1000 m), mid-elevations (1000 - 2000 m), and highlands (> 2000
 696 m). Species could also occur in more than one elevational band which adds three
 697 more categories: low-mid, mid-high and full range (i.e., species living from lowlands to
 698 highlands).

				Old	New
Elevation	Total	Temperate	Tropical	World	World
High	79	27	52	35	44
Mid-High	406	90	316	179	227
Mid	126	13	113	63	63
Low-Mid	2140	314	1826	1367	773
Low	2561	306	2255	1392	1169
Full-range	394	133	261	240	154
Total	5706	883	4823	3276	2430

699

700

701 **Supplementary Table 2.** Summary of linear models of tip-DR as function of
 702 elevation, latitude and their interaction. In models with shared ancestry, species are
 703 no longer statistically independent observations in the calculation (i.e., Phylogenetic
 704 Generalized Least Squares), in contrast to models where the evolutionary history of
 705 species is ignored.

706

Model	Shared ancestry	F-statistic	Overall probability
Elevation + Latitud + Interaction	no	16.11	p < 0.001
Elevation + Latitud + Interaction	yes	0.8149	p = 0.485
Elevation + Latitud	no	18.6	p < 0.001
Elevation + Latitud	yes	0.7144	p = 0.485
Elevation	no	17.15	p < 0.001
Elevation	yes	1.413	p = 0.234
Latitud	no	16.53	p < 0.001
Latitud	yes	0.019	p = 0.887

707

Supplementary Table 3. Models of passerine diversification depending on elevation while accounting for potential latitudinal and longitudinal differences (i.e. temperate - tropical and temperate - tropical regions). Speciation or extinction can depend on the elevational range (Elevation-Dependent; ED), or on an unknown trait (Concealed Trait-Dependent; CTD). A model with Constant Rates (CR) across lineages is also included. Models assume explicit constraints (Uphill-Downhill and Expansion-Contraction) on how lineages disperse across elevations over evolutionary time. The fourth column shows whether the examined and concealed traits are assumed to transit at the same rates. When latitudinal analysis is indicated in the fifth column, latitudinal state was incorporated in the secsse analyses (Partial Loglikelihood) whereas longitude was analyzed separately under a simple model of trait evolution and added to obtain the Total Loglikelihood. Likewise, when Longitudinal analysis is indicated, latitude was analyzed separately (see Methods). When Global is indicated, a model of trait evolution that considers the transitions across Latitude and Longitude were analyzed separately. For each model, the number of free parameters k is indicated, AIC weights and Δ AIC values are computed using Total Loglikelihoods and used to compare models. Best performing latitudinal, longitudinal and global models are highlighted in gray.

Trait-dependence	Elevation mode	transition	Variability across state	Qexamined = Qconcealed?	Type of analysis	Partial Loglikelihood	Total Loglikelihood	k	AICw	Δ AIC
CTD	Uphill-Downhill		Speciation	No	Latitudinal	-26730.47	-26785.54	12	~ 0.99	0

CTD	Uphill-Downhill	Speciation	Yes	Latitudinal	-26856.93	-26912.00	9	< 0.0001	247
ED	Uphill-Downhill	Speciation	Yes	Latitudinal	-27069.99	-27125.06	9	< 0.0001	673
ED	Uphill-Downhill	Speciation	No	Latitudinal	-27070.06	-27125.13	12	< 0.0001	679
CR	Uphill-Downhill	Speciation	Yes	Latitudinal	-27287.98	-27343.05	6	< 0.0001	1103
ED	Uphill-Downhill	Extinction	Yes	Latitudinal	-27287.94	-27343.01	9	< 0.0001	1109
CR	Uphill-Downhill	Speciation	No	Latitudinal	-27307.17	-27362.24	9	< 0.0001	1147
CTD	Uphill-Downhill	Extinction	No	Latitudinal	-27310.58	-27365.65	12	< 0.0001	1160
ED	Uphill-Downhill	Extinction	No	Latitudinal	-27329.65	-27384.72	12	< 0.0001	1198
CTD	Uphill-Downhill	Speciation	No	Global	-24927.06	-27418.86	10	< 0.0001	1263
CTD	Uphill-Downhill	Extinction	Yes	Latitudinal	-27409.29	-27464.36	9	< 0.0001	1352
CTD	Uphill-Downhill	Speciation	Yes	Global	-24980.61	-27472.41	8	< 0.0001	1366
CTD	Expansion-Contraction	Speciation	No	Latitudinal	-27735.41	-27790.48	12	< 0.0001	2010
CTD	Expansion-Contraction	Speciation	No	Global	-25322.63	-27814.43	10	< 0.0001	2054
CTD	Expansion-Contraction	Speciation	Yes	Global	-25335.06	-27826.86	8	< 0.0001	2075
ED	Uphill-Downhill	Speciation	Yes	Global	-25336.69	-27828.49	8	< 0.0001	2078
ED	Uphill-Downhill	Speciation	No	Global	-25336.94	-27828.74	10	< 0.0001	2082
CTD	Uphill-Downhill	Speciation	No	Longitudinal	-25491.37	-27928.10	12	< 0.0001	2285

CTD	Expansion-Contraction	Speciation	Yes	Latitudinal	-27877.70	-27932.77	9	< 0.0001	2288
CR	Uphill-Downhill	Speciation	Yes	Global	-25472.91	-27964.72	6	< 0.0001	2346
ED	Uphill-Downhill	Extinction	Yes	Global	-25472.88	-27964.68	8	< 0.0001	2350
CR	Uphill-Downhill	Speciation	No	Global	-25472.91	-27964.72	8	< 0.0001	2350
CTD	Uphill-Downhill	Extinction	Yes	Global	-25472.92	-27964.72	8	< 0.0001	2350
ED	Uphill-Downhill	Extinction	No	Global	-25472.88	-27964.68	10	< 0.0001	2354
CTD	Uphill-Downhill	Extinction	No	Global	-25476.31	-27968.11	10	< 0.0001	2361
CTD	Uphill-Downhill	Speciation	Yes	Longitudinal	-25548.50	-27985.23	9	< 0.0001	2393
ED	Expansion-Contraction	Speciation	Yes	Latitudinal	-28191.26	-28246.33	9	< 0.0001	2916
ED	Expansion-Contraction	Speciation	Yes	Global	-25756.98	-28248.78	8	< 0.0001	2918
ED	Expansion-Contraction	Speciation	No	Global	-25766.41	-28258.21	10	< 0.0001	2941
ED	Expansion-Contraction	Speciation	No	Latitudinal	-28218.90	-28273.97	12	< 0.0001	2977
ED	Uphill-Downhill	Speciation	Yes	Longitudinal	-25848.43	-28285.16	9	< 0.0001	2993
ED	Uphill-Downhill	Speciation	No	Longitudinal	-25870.24	-28306.97	12	< 0.0001	3043
ED	Expansion-Contraction	Extinction	No	Global	-25830.22	-28322.02	10	< 0.0001	3069
CR	Expansion-Contraction	Speciation	Yes	Global	-25841.22	-28333.02	6	< 0.0001	3083
ED	Expansion-Contraction	Extinction	Yes	Global	-25840.72	-28332.52	8	< 0.0001	3086

CR	Expansion-Contraction	Speciation	No	Global	-25841.22	-28333.02	8	< 0.0001	3087
CTD	Expansion-Contraction	Extinction	Yes	Global	-25841.23	-28333.03	8	< 0.0001	3087
CTD	Expansion-Contraction	Extinction	No	Global	-25841.24	-28333.04	10	< 0.0001	3091
CTD	Expansion-Contraction	Speciation	Yes	Longitudinal	-25914.45	-28351.18	9	< 0.0001	3125
CTD	Expansion-Contraction	Speciation	No	Longitudinal	-25923.45	-28360.18	12	< 0.0001	3149
ED	Expansion-Contraction	Extinction	Yes	Latitudinal	-28309.92	-28364.99	9	< 0.0001	3153
CR	Expansion-Contraction	Speciation	Yes	Latitudinal	-28424.00	-28479.07	6	< 0.0001	3375
ED	Expansion-Contraction	Extinction	No	Latitudinal	-28420.98	-28476.05	12	< 0.0001	3381
CR	Expansion-Contraction	Speciation	No	Latitudinal	-28424.00	-28479.07	9	< 0.0001	3381
CTD	Expansion-Contraction	Extinction	Yes	Latitudinal	-28424.01	-28479.08	9	< 0.0001	3381
CR	Uphill-Downhill	Speciation	Yes	Longitudinal	-26047.86	-28484.59	6	< 0.0001	3386
CTD	Expansion-Contraction	Extinction	No	Latitudinal	-28424.00	-28479.07	12	< 0.0001	3387
CR	Uphill-Downhill	Speciation	No	Longitudinal	-26047.87	-28484.60	9	< 0.0001	3392
ED	Uphill-Downhill	Extinction	No	Longitudinal	-26047.69	-28484.42	12	< 0.0001	3398
CTD	Uphill-Downhill	Extinction	No	Longitudinal	-26047.91	-28484.64	12	< 0.0001	3398
ED	Uphill-Downhill	Extinction	Yes	Longitudinal	-26075.04	-28511.77	9	< 0.0001	3446
CTD	Uphill-Downhill	Extinction	Yes	Longitudinal	-26113.74	-28550.47	9	< 0.0001	3524

ED	Expansion-Contraction	Speciation	Yes	Longitudinal	-26403.33	-28840.06	9	< 0.0001	4103
ED	Expansion-Contraction	Speciation	No	Longitudinal	-26409.87	-28846.60	12	< 0.0001	4122
ED	Expansion-Contraction	Extinction	Yes	Longitudinal	-26515.80	-28952.53	9	< 0.0001	4328
CR	Expansion-Contraction	Speciation	Yes	Longitudinal	-26574.03	-29010.76	6	< 0.0001	4438
CR	Expansion-Contraction	Speciation	No	Longitudinal	-26574.03	-29010.76	9	< 0.0001	4444
CTD	Expansion-Contraction	Extinction	Yes	Longitudinal	-26574.03	-29010.76	9	< 0.0001	4444
ED	Expansion-Contraction	Extinction	No	Longitudinal	-26572.24	-29008.97	12	< 0.0001	4447
CTD	Expansion-Contraction	Extinction	No	Longitudinal	-26574.03	-29010.76	12	< 0.0001	4450

Supplementary Table 4. Models of passerine diversification depending on elevation while considering the spatial configuration of lowlands. Speciation or extinction can depend on the elevational range (Elevation-Dependent; ED), or on an unknown trait (Concealed Trait-Dependent; CTD). A model with Constant Rates (CR) across lineages is also included. Models assume explicit constraints (Uphill-Downhill and Expansion-Contraction) on how lineages disperse across elevations over evolutionary time. Different from the analysis shown in Extended Data Table 3, the models we compare in this table include an additional state (L-) which represents those lineages that cannot colonize higher elevations (i.e., island species or species far from mountain ranges). In this model, only Lowland species (see Figure 2) can expand their distribution uphill and lineages in L- need first to colonize lowlands to then move to higher elevation. In this model, the rates of moving across elevations (or contracting/expanding) are different from shifting from L- to Lowlands (and the reverse) as they are different processes. The fourth column shows whether the rates from L- to Lowlands are different than from Lowlands to L-. For each model, the number of free parameters k is indicated and AIC weights are computed to compare models.

Trait-dependence	Elevation transition mode	Variability	Asymmetric	Loglikelihoods	k	AICw
		across state	Foothill Dispersal			
CTD	Uphill-Downhill	Speciation	Yes	-25313.8	8	~ 0.99
CTD	Uphill-Downhill	Speciation	No	-25464.8	7	< 0.0001
CTD	Expansion-Contraction	Speciation	Yes	-25813	8	< 0.0001
ETD	Uphill-Downhill	Speciation	Yes	-25856.5	8	< 0.0001
CTD	Uphill-Downhill	Extinction	Yes	-25938.3	8	< 0.0001

CR	Uphill-Downhill	Speciation	Yes	-26005	6	< 0.0001
ETD	Uphill-Downhill	Extinction	Yes	-26004.9	8	< 0.0001
CTD	Expansion-Contraction	Speciation	No	-26020.4	7	< 0.0001
ETD	Uphill-Downhill	Speciation	No	-26026.3	7	< 0.0001
CR	Expansion-Contraction	Speciation	No	-26553.6	5	< 0.0001
CR	Expansion-Contraction	Speciation	Yes	-26349.8	6	< 0.0001
CR	Uphill-Downhill	Speciation	No	-26162.5	5	< 0.0001
CTD	Expansion-Contraction	Extinction	No	-26437.6	7	< 0.0001
CTD	Expansion-Contraction	Extinction	Yes	-26257.6	8	< 0.0001
CTD	Uphill-Downhill	Extinction	No	-26074.6	7	< 0.0001
ETD	Expansion-Contraction	Speciation	No	-26458.7	7	< 0.0001
ETD	Expansion-Contraction	Speciation	Yes	-26263.6	8	< 0.0001
ETD	Expansion-Contraction	Extinction	No	-26285.5	7	< 0.0001
ETD	Expansion-Contraction	Extinction	Yes	-26066.3	8	< 0.0001
ETD	Uphill-Downhill	Extinction	No	-26159.3	7	< 0.0001