University of Groningen

Evolutionary dynamics of the elevational diversity gradient in passerine birds

van Els, Paul; Herrera-Alsina, Leonel; Pigot, Alex L.; Etienne, Rampal S.

Published in:
Nature Ecology and Evolution

DOI:
[10.1038/s41559-021-01515-y](https://doi.org/10.1038/s41559-021-01515-y)

IMPORTANT NOTE: You are advised to consult the publisher's version (publisher's PDF) if you wish to cite from it. Please check the document version below.

Document Version
Publisher's PDF, also known as Version of record

Publication date:
2021

[Link to publication in University of Groningen/UMCG research database](#)

Citation for published version (APA):

van Els, P., Herrera-Alsina, L., Pigot, A. L., & Etienne, R. S. (2021). Evolutionary dynamics of the elevational diversity gradient in passerine birds. *Nature Ecology and Evolution*, 5(9), 1259-1265. <https://doi.org/10.1038/s41559-021-01515-y>

Copyright

Other than for strictly personal use, it is not permitted to download or to forward/distribute the text or part of it without the consent of the author(s) and/or copyright holder(s), unless the work is under an open content license (like Creative Commons).

The publication may also be distributed here under the terms of Article 25fa of the Dutch Copyright Act, indicated by the "Taverne" license. More information can be found on the University of Groningen website: <https://www.rug.nl/library/open-access/self-archiving-pure/taverne-amendment>.

Take-down policy

If you believe that this document breaches copyright please contact us providing details, and we will remove access to the work immediately and investigate your claim.

Downloaded from the University of Groningen/UMCG research database (Pure): <http://www.rug.nl/research/portal>. For technical reasons the number of authors shown on this cover page is limited to 10 maximum.

Evolutionary dynamics of the elevational diversity gradient in passerine birds

Paul van Els^{1,3,5}, Leonel Herrera-Alsina^{1,4,5}✉, Alex L. Pigot^{2,6} and Rampal S. Etienne^{1,6}

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

The striking differences in the form and diversity of life as one travels up mountains is one of the most prominent and long-recognized patterns in biogeography¹. Across animals and plants, and across mountains globally, diversity tends to peak at low or intermediate elevations and then declines towards mountain summits^{2,3}. Thus, while mountain regions are global hotspots of diversity^{4,5}, most species occur in the lowlands, with relatively few species in the highlands. One possible explanation for this global elevational diversity gradient (EDG) is that for most groups of organisms, there has been more time for species to accumulate at low to intermediate elevations, with highland environments only colonized more recently⁶. Another, but not mutually exclusive, possibility is that net rates of diversification are faster in the lowlands, because the greater area or energy availability increases the ecological limit to diversity or promotes faster intrinsic rates of speciation and lower extinction⁷. Yet there is also evidence that highland regions may be cradles of species diversity, characterized by exceptionally fast rates of speciation^{8,9}. In other words, speciation may be fastest at high elevations, even though species diversity is currently lowest there³. This suggests a third possible factor contributing to the EDG: species generated in disproportionately larger numbers in the highlands migrate to the lowlands.

Macroecological studies of current species distribution patterns have long supported the idea that highlands may be hotbeds of evolution, especially in the tropics¹⁰. Large numbers of endemic species are concentrated on tropical mountains—far more than would be expected by chance or current climate¹¹. More-recent phylogenetic studies have shown that many of these endemic species are comparatively young, pointing towards rapid speciation^{12,13}. There are various reasons why rates of speciation may be faster at high elevations, including the fragmentation of habitats on different

mountain summits¹³; ecological opportunity as new habitats were made available during recent mountain uplift¹⁴; exposure to higher levels of ultraviolet radiation, which boosts rates of mutation¹⁵; and the susceptibility of species inhabiting narrow thermal bands to becoming isolated by the expansion of glaciers during recurring ice ages^{12,16}. All of these factors are thought to be particularly important in the tropics because limited seasonal variation enables the greater thermal stratification of species across mountain slopes, enhancing opportunities for geographic isolation and divergent ecological selection¹⁷. However, while some studies have supported the idea that diversification is faster in the highlands¹⁸, other studies have found no evidence for differences in diversification rates across elevations¹⁹, and thus whether rates of diversification vary consistently across elevations remains debated.

One explanation for this lack of resolution is that the dynamics of the EDG may be highly variable, differing between mountain regions with contrasting geological histories and geographic properties²⁰. For instance, some highland lineages in the Andes have undergone explosive radiations, but such cases appear to be less common in mountain systems in the Afrotropics²⁰. In addition, gradients in diversity—as well as the phylogenetic branching times that are used to model these gradients—arise not only from differences in diversification but also from the dispersal of lineages across elevations. Yet models that account for both differences in diversification and the movement of species between elevational bands have rarely been applied. Some verbal models predict that highland communities are evolutionary sinks, derived primarily from the lowland taxa either invading or being passively transported to higher elevations during mountain uplift²¹. Other verbal models predict that highland regions act as species pumps, with lineages arising at higher elevations moving downslope^{21–25}, providing an important contribution

¹Groningen Institute for Evolutionary Life Sciences, University of Groningen, Groningen, The Netherlands. ²Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and Environment, University College London, London, UK. ³Present address: Sovon Dutch Centre for Field Ornithology, Nijmegen, The Netherlands. ⁴Present address: School of Biological Sciences, University of Aberdeen, Aberdeen, UK. ⁵These authors contributed equally: Paul van Els, Leonel Herrera-Alsina. ⁶These authors jointly supervised this work: Alex L. Pigot, Rampal S. Etienne.

✉e-mail: leonelhalsina@gmail.com

Fig. 1 | The global EDG in passerine birds. a, Species richness in birds exhibits a decline with elevation. The three assigned elevational bands (altitudinal delimitation for temperate regions is in brackets) and six possible elevational states of species are shown, with the number of species in each state indicated. States account for species that are restricted to a single elevational band or that span multiple elevational bands. **b**, The distribution of species across elevational bands within the passerine phylogenetic tree, with elevation states plotted concentrically onto the phylogeny. Colours match those in **a**.

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

Here we study the dynamics of the EDG of passerine birds, a global ‘super radiation’ of exceptional diversity, including approximately 5,700 species, found at almost all elevations, latitudes and biogeographic realms (other than Antarctica). Passerines have arisen in approximately the last 47 million years²⁶, and represent an ideal study group. Passerines show a clear EDG, with over eight times as many species present in the lowlands ($n=5,095$, lower elevation bound < 1,500 m) as there are mid-elevation (> 1,500 m) or high-elevation (> 3,000 m) specialists combined ($n=611$) (Fig. 1 and Supplementary Table 1). The sheer diversity of passerines, combined with the availability of phylogenetic trees²⁷, provides substantial power for comparing competing scenarios of diversification and dispersal between different elevational bands (Fig. 1). Notably, although characterizing the distribution of species in topographically diverse regions is challenging, the elevational ranges of passerines are relatively well-known, with estimates of upper and lower elevation limits available for almost all (96%) species.

Using this dataset, we first examine the relationship across passerines between the elevational state of a species and its tip diversification rate (tip-DR) metric, which reflects speciation rate²⁸ and has previously been applied to test for latitudinal and elevation gradients in avian evolutionary rates³. Because this metric does not account for the movement of species between elevational bands, we then apply a recently developed dynamic phylogenetic model (several examined and concealed states-dependent speciation and extinction; SecSSE²⁹), which, in addition to testing for elevation-dependent rates of speciation and extinction, also enables us to account for the transition of species between different elevational states over evolutionary time. Using this dynamic model, we are also able to test whether species movement downhill is faster or slower than the rate of movement uphill, and thus whether high-

lands act a source or sink of species diversity, respectively. Finally, because there is evidence that rates of diversification in passerines may vary between the tropics and the temperate zone³⁰ and between the New World and the Old World²⁷, we allow rates of speciation (or extinction) to vary between either different longitudinal (Old and New World) or different latitudinal (tropics and temperate) regions, when testing for an effect of elevation (Fig. 2).

Results

Diversification and dispersal across elevations. When comparing the tip-DR of species currently occurring in the lowlands and the highlands, rates of speciation are inferred to be slightly but significantly faster in the highlands. This is consistent with previous assemblage-level analyses, indicating that the average tip-DR of highland bird assemblages is greater than that of lowland bird assemblages³. However, closely related species show a strong tendency to share similar tip-DR values (Pagel’s $\lambda=0.98$, 95% confidence interval: 0.98–0.99), and thus any association between elevation and speciation rate could be driven by phylogenetic non-independence. In accordance with this, when shared ancestry is accounted for with a phylogenetic generalized linear model, the relationship between elevation and tip-DR disappears (Supplementary Table 2).

Although this result suggests that there is no association between elevation and speciation rate, this analysis must be interpreted with caution, because it assumes that species distributions are static, and thus it does not account for the movement of species between different elevational bands over evolutionary time. To address this shortcoming, we next fitted a dynamic model that estimates the diversification rate associated with each elevational state as well as the transition rates between these states. We compared the fit of a model in which rates of speciation (or extinction) vary across elevation to two alternative null models. First, a constant-rate model, in which all lineages share an identical rate of diversification. Second, a concealed-trait-dependent (CTD) model, in which rates of diversification are allowed to vary across lineages owing to ‘hidden’ variation, but they do so independently of elevation. This second null model is more realistic because it accounts for the possibility that rates of diversification have been heterogeneous across passerines,

Fig. 2 | The dynamics of the EDG are modelled by allowing rates of diversification to vary across the elevational states of species and by allowing transitions between different elevational states over time. We model transitions between states by considering that species contract their elevational range when they become absent from an elevational band and expand their elevational range when they become present in a new elevational band. We consider two possible scenarios of how species transition between elevational states. **a**, First, in the uphill–downhill scenario, the rate of transition to a higher elevational state can differ from the rate of transition to a lower elevational state. **b**, Second, in the expansion–contraction scenario, the transition to a wider elevational state (that is, present in more elevational bands) can differ from the rate of transition to a narrower elevational state (that is, present in fewer elevational bands). **c**, In addition to transitions between elevational states, species may also transition between different biogeographic states, indicated by their presence in either the Old World or the New World, or in the temperate zone or the tropical zone. We show the per-lineage rates (per Myr) of transition across longitude, latitude and elevation that maximize the likelihood of the best-supported model.

and means that support for elevation-dependent rates of diversification does not arise simply because of the unrealistic assumption of a constant rate of diversification across such a large clade.

When compared to a standard constant-rate null model, in which rates of diversification are equal across elevational states, an elevation-dependent model, in which rates of diversification increase with elevation, is more strongly supported. This result seemingly supports previous analyses suggesting faster rates of bird diversification in the highlands³. However, when compared to a CTD null model, in which rates of diversification are allowed to vary across lineages but independently of elevation, the CTD null model is overwhelmingly supported (Akaike information criterion (AIC) weight ~ 0.99). Thus, while our results provide substantial support for a scenario in which diversification rates vary across lineages, this variation is likely to be due to other factors than elevation (Supplementary Table 3). The best-supported model is a latitudinal-CTD model, in which rates of speciation are 1.4 times faster in the tropics than in the temperate zone. Across all models,

extinction is estimated to be low (latitudinal-CTD model, $\mu = 0.0001$ per Myr) and a latitudinal-CTD model with heterogeneity in rates of speciation is more strongly supported than a CTD model with heterogeneity in rates of extinction across lineages and/or regions. Finally, we find no evidence for differences in rates of diversification between the Old World and the New World (Supplementary Table 3).

Although we find no effect of elevation on rates of diversification, we find substantial differences in rates of downhill and uphill dispersal. According to the best model, the estimated per-lineage rate of downhill dispersal is 0.189 per Myr—substantially faster than the uphill dispersal rate of 0.072 per Myr (Fig. 2). This model of faster downhill dispersal is much more strongly supported than an alternative expansion–contraction scenario, in which rates of elevational range expansion and contraction may differ, but there is no difference between uphill and downhill movement (Fig. 2). The best-supported model allows transition rates between elevational states to differ from those of the transition rates between the concealed-trait states, rather than assuming that these are identical (Supplementary Table 3), even though the former model has more parameters. We find, as may be expected, that lineages disperse between continents at rates that are lower than those for dispersal across elevational bands. The best model shows that the rate of lineage exchange between the tropics and the temperate zone is 0.0187 per Myr, with lineage dispersal between the Old World and the New World occurring at a rate of 0.00016 per Myr (Fig. 2). Note that all of these rates are per-lineage rates.

Most passerines are tropical and so to test whether our results hold when using a tropical subgroup, we repeated our analysis focusing on the ovenbirds, a large tropical radiation ($n = 285$ species). Ovenbirds are spread across latitudinal bands in similar proportions to the entire dataset, they inhabit only the New World tropical region, and a high-quality and comprehensively sampled phylogenetic tree is available³¹. The results for ovenbirds are consistent with those from the global analysis, with no evidence of differences in diversification across elevation, and the uphill–downhill model receiving the highest support, with the rate of downhill dispersal (0.3176) substantially exceeding the rate of uphill dispersal (0.1538).

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

Geographic origin of passerines and accumulation of lineages over time. Because the elevational origin of passerines can have an important influence on the current gradient of species richness, we extracted the probabilities (using the best-supported model) of each state (that is, the combination of elevation and latitude) at the most-basal node of the phylogeny to estimate where the clade first appeared. These probabilities indicate the most likely state of the ancestral species just before it splits at the crown of the phylogeny, and so the true origin of the clade (at the stem age) may have been different. Regardless of whether rates of diversification are allowed to vary with latitude or longitudinal region, a highland origin of passerines is equally well supported as a lowland origin. This lack of strong support for either elevational state reflects the relatively rapid transitions across elevation that are inferred by our analysis

and which have likely erased this historical signal of where passerines originated.

Discussion

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

The absence of a consistent effect of elevation on diversification is unlikely to be explained by a lack of statistical power. Our analysis contains thousands of species and our model did detect faster rates of diversification in the tropics compared to the temperate zone. This suggests that if there were a globally coherent effect of elevation on diversification, this would also have been detected in our analysis. Furthermore, the absence of any effect of elevation on diversification cannot be explained by a failure of our model to detect finer-scale heterogeneity in diversification rates within the tropics or the temperate zone. The strong support for the CTD model confirms that there is indeed substantial heterogeneity in rates of diversification across passerines within these regions, but that this variation is not aligned with elevation. Critically, our results show that failure to account for this background heterogeneity in rates of diversification would have led to the spurious conclusion that rates of diversification do increase with elevation. We therefore suggest that application of such a CTD model is an important advance that should also be applied when examining other putative drivers of diversification rates (for example, body size).

One possible explanation for why our global analysis does not detect an elevational gradient in diversification is that different dynamics may prevail in different regions, obscuring the overall importance of elevation. Differences across latitude may be particularly important in this regard, because it is mainly highlands in the tropics where rates of speciation are thought to be promoted³². However, this is unlikely to explain our results because most of the species in our analysis (85%) occur in the tropics, and thus it is the dynamics of the EDG in this region that dominate our model inferences. Indeed, our results based on the tropical ovenbirds are highly consistent with the general pattern. Rather, our results suggest that net rates of diversification are boosted in the tropics, but that this occurs regardless of elevation.

Another possibility is that although diversification and elevation may be related in some mountain systems, these effects of elevation are highly context dependent, determined by the particular geological history and environment in different mountains³. Accounting for such variability is challenging because it would require a substantial increase in model complexity and the number of parameters that need to be inferred. We note that support for such a complex model would not alter our main conclusion that, at a global scale, there is no consistent trend in diversification across elevation.

Our finding that net rates of diversification in passerines do not vary consistently with elevation contrasts with the results of a recent study showing that diversification rates increase with elevation³. We note a number of important methodological differences that may explain these contrasting findings. In the other study, speciation rate was calculated for each extant bird species (tip-DR) and this was then averaged across all of the species inhabiting each elevational band across major mountain systems. This approach strongly differs from ours, because it mainly captures recent speciation and because it links the speciation rate of a lineage to its current elevation. This method ignores dispersal across elevational bands and

thus the possibility that the speciation events leading to a particular lineage occurred at a different elevation to the elevation at which that species currently resides. Furthermore, while the shared phylogenetic history of each species is automatically accommodated in our dynamic model (that is, each branch of the tree is only counted once), our results show that treating each species as statistically independent when analysing tip-DR may lead to spurious results. On the basis of these results, we suggest that accounting for the biogeographic dynamics and phylogenetic non-independence of lineages is likely to be critical when making inferences of how rates of diversification vary across elevation or any other gradient.

Much of the research on the evolutionary dynamics of the EDG has focused on explaining patterns at relatively fine taxonomic scales or particular mountain systems. Although these have provided evidence for both uphill³³ and downhill³⁴ movement of species, they have often supported the idea that most clades originated in the lowlands and then invaded higher elevations³⁵. For example, among avian genera, *Leptopogon* flycatchers²³, chat-tyrants²⁵, *Andropadus* greenbuls²⁴ and *Thamnophilus* antshrikes³⁶ show a repeated movement of species into the highlands followed by in situ diversification. Larger and older clades, however, paint a more complex picture, with a study³⁵ providing evidence that hummingbirds (Trochilidae) have undergone multiple colonizations of the Andes from the lowlands, but also the reverse. Our findings across passerines place these previous genus- and family-level studies in a broader context, showing that while there are many cases of uphill dispersal followed by radiation, overall, on a per-lineage basis, the dispersal from high to low elevations occurs at a much faster rate.

Why per-lineage rates of dispersal from highlands to lowlands are faster than the reverse remains unclear. Indeed, most studies have suggested a net movement of species uphill, because of either ecological opportunity¹⁴ or passive transportation during mountain uplift²¹. A non-biological explanation of higher rates of dispersal downhill than uphill could be that available area decreases with elevation, which allows more species to fit in the lowlands. Another possible mechanism is that strong physiological limitations prevent adaptation to higher elevations (that is, ultraviolet radiation and oxygen availability vary across altitude). For instance, bird species living at high altitude show a loss of genes related to the immune response and require a specific machinery to repair cellular damage caused by ultraviolet radiation³⁷. Lineages adapting to highlands and losing immune function might be unlikely to regain it. However, the return to lowlands or the adaptation to lowlands by highland-originated lineages could be mediated by a stronger expression of the immune response boosted by high levels of oxygen³⁸. In addition, decreased oxygen concentration can severely increase the chances of hypoxia during flight³⁹. Although phenotypic plasticity could partially tackle this limitation⁴⁰, evolutionary adaptations involving changes in the affinity of haemoglobin for oxygen may be difficult to develop as there are few molecular pathways that are not associated with reduced fitness (that is, deleterious pleiotropic effects)⁴¹. Furthermore, species that are adapted to a low concentration of oxygen require large lungs that are costly to maintain so the switch to a lowland region might be beneficial from an energetic standpoint⁴². It is important to note that we are reporting the rates of successful dispersal events between elevational bands and that dispersal events not leading to establishment are not recorded. Hence, another alternative is that high-elevation habitats may be less conducive to colonization over macroevolutionary timescales⁴³ owing to ecological constraints—that is, a lower availability of resources⁷. In other words, it is possible that lineages are equally likely to disperse regardless of the elevation from which they arise, but those elevational bands in which the niche space is wider are more likely to accommodate colonizers⁴⁴. Thus, our results are potentially consistent with the idea that higher ecological limits to

coexistence in the lowlands ultimately underlie the EDG in passerine birds⁴⁵.

Our results provide support for the idea that highland regions have acted as a species pump for passerine birds, not because of faster total rates of diversification, but because species arising in the highlands disperse downhill. Thus, although highlands constitute only a fraction of passerine diversity they play a disproportionate role in boosting the diversity of the lowlands. Highland species are at particular risk of extinction from anthropogenic warming this century, owing to a lack of available cooler habitats to which species can disperse⁴⁶. Our results suggest that the loss of highland lineages will also have long-term impacts on the diversity of the lowlands and passerines globally.

Methods

Phylogenetic framework. We used a Bayesian pseudo-posterior distribution of time-calibrated phylogenies⁴⁷, which includes 9,993 of 10,473 currently recognized bird species. Using the program TreeAnnotator from the BEAST2 package v.2.4.2 (ref. 47), we produced a maximum-clade credibility tree from all available stage-2 trees with the Hackett backbone. We pruned this tree to the level of Passeriformes ($n = 5,966$ species). We are aware of the shortcomings of using a megaphylogeny that does not include sequence data for each taxon⁴⁸, but the statistical power achieved by the large number of tips and branching events compensates, at least in part, for the possible lack of taxonomic precision. To test whether our results hold in a subset, we repeated our analysis using a phylogeny for ovenbirds (Furnariidae) for which 97% of species have been sequenced³¹.

Elevation data and large-scale realms. We compiled elevation data for passerines, recording lower and upper elevation bounds of their distribution, on the basis of descriptions in the Handbook of the Birds of the World⁴⁹. We did not include occasional records at extreme elevation. Elevational distributions are based on the breeding range, thus excluding wintering and transient elevation records. Species without known elevational distribution were assigned NA in the dataset ($n = 260$) rather than removed, because this could bias diversification rates, and our analysis can account for this missing data.

Our model of elevation-dependent diversification and dispersal requires treating elevation as a categorical state. To do this we defined three elevational bands whose altitudinal range vary latitudinally. In tropical regions: lowlands (from sea level up to 1,500 m above sea level), mid-elevations (1,500–3,000 m) and highlands (>3,000 m). In temperate regions: lowlands (from 0–1,000 m), mid-elevations (1,000–2,000 m) and highlands (>2,000 m). These categories broadly agree with those established previously⁵⁰ for Neotropical montane birds based on the dominant vegetation associated with the tropics, subtropics and alpine zones, respectively. Species may inhabit multiple bands (indeed, some species span the entire elevation gradient) and accounting for this variation in elevational range size is important when determining the dynamics of the EDG. We therefore defined three additional categories for species that inhabit more than one elevational band: low–mid, mid–high and full range (that is, species living from lowlands to high-montane areas). The number of species in each category is shown in Supplementary Table 1. From hereon we refer to these six elevational categories as the elevational state of the species. While this was our main dataset, we formulated another dataset in which the lowlands category was split between lowlands that are adjacent to mountains and lowlands that are not adjacent to mountains.

We first performed a global analysis in which rates of diversification depend on elevation, resulting in six states. We then accounted for the possibility that rates of diversification may differ across latitude and longitude in the following way. We distinguished species occurring in the tropics from species in the temperate zone (latitudinal analysis), so that latitude and elevation can differentially affect diversification, resulting in a model with 12 states (for example, a species could be a tropical lowland species, or in a temperate mid–high state). We classified species as tropical when most of the latitudinal span of their breeding distribution⁴⁹ lies between the tropics of Cancer and Capricorn. Finally, we distinguished Old World from New World species (longitudinal analysis), again resulting in 12 possible states (for example, Old World low–mid state), in which longitude and elevation can differentially affect diversification. We did not perform an analysis in which diversification rates simultaneously depend on elevation, latitude and longitude, because the large state space required for such an analysis was computationally unfeasible and numerically unstable given the size of our phylogeny (see next section).

State-dependent diversification analysis and parameterization. We used the SSE framework, which allows the determination of whether diversification rates are associated with an evolving trait⁵¹. In this model, the speciation rate (λ_i) or extinction rate (μ_i) of a lineage depends on its trait state i (here elevation, or a combination of elevation and latitude (tropical or temperate) or longitude (New

World or Old World)). To keep the number of estimated parameters as low as possible during the likelihood optimization, we only optimized the speciation (or extinction) rate of the low-, mid- and high-elevation state and used these values to obtain average rates for the states that are a combination of those elevations (for example, the low- and mid-elevation rates of speciation are averaged to yield the rate of the low–mid-elevation state).

The state of a species is not static, with species switching to a different state at rate q_{ij} , where i and j represent the state of origin and the state of destination, respectively. This allows us to use trait and branching patterns simultaneously to study macroevolutionary dynamics. In other words, when lineages living in different elevational states experience different speciation or extinction regimes, the shift from one elevational state to another will have an effect on diversification rates. Statistical support for elevation affecting diversification rates is found when the likelihood of a model in which speciation (or extinction; see below) differs across elevational states (elevation-dependent model) is higher—after correcting for differences in numbers of parameters—than a model in which rates depend on an unknown (hidden or concealed) trait (CTD model) and a model with constant rates (constant-rate model)^{29,52}. The comparison in terms of likelihood between elevation-dependent and CTD models is important to prevent spurious conclusions regarding the association between heterogeneity in diversification rates across lineages and the evolution of the trait. We used the R package 'scesse' (ref. 29), which computes and optimizes the likelihood of the model with two or more states.

We assume that species transition between elevational states via the expansion into an adjacent elevational band (that is, from low to low–mid or from high to mid–high) or from contraction at the edge of the range (that is full range to low–mid or mid–high). In other words, we do not allow disjunct elevational ranges as these are rarely observed⁷. We considered two alternative scenarios for how rates of transitions between states may vary. In both cases we estimate two transition rates. First, under an uphill–downhill model, uphill transitions have a different rate than downhill transitions. Note that under the uphill–downhill scenario, changing from, for example, the low–mid-elevation state to the low-elevation state means going downhill. Second, under an expansion–contraction model, all expansion rates (that is, change from one single elevational band to two, or from two to three) are equal but different from contraction rates (that is, a change from two bands to a single band, or from three to two bands), which are also equal. We implemented the expansion–contraction model because it allows us to test a scenario in which the rate at which species colonize or become extinct at a particular elevation can differ, but in which these rates are independent of elevational direction. In other words, in contrast to the uphill–downhill model, colonizing (or becoming extinct at) a lower or higher elevational band is equally likely. As recommended previously²⁹, for the concealed trait we assumed an identical model structure, in terms of the number of states and possible transitions between these. We implemented two versions of the CTD model: one in which the transition rates between concealed states are the same as those between elevational states, and one in which we relax this assumption and allow the transition rates of the concealed trait to be different from the transition rates between elevational bands. Because differences in diversification rates across elevations could be due to either differential speciation or differential extinction, we ran all the mentioned model combinations with two different assumptions: in speciation-dependent diversification, speciation varied across states while extinction remained constant. For extinction-dependent diversification, extinction was free to vary across states whereas speciation was kept constant.

In the analysis in which we added the state L^- that accounts for those lowland species that have limited access to mountain ranges, only lowland species could expand their distribution uphill. Lineages in L^- need first to colonize lowlands close to mountains (L) to then move to higher elevation. In this model, we allow the rates of moving across elevations (or contracting or expanding) to be different from shifting from L^- to L (and the reverse) as they are different processes. Uphill–downhill and expansion–contraction model structures are the same as in the global analysis. We ran two versions of this model, one in which the rates from L^- to L are different to those from L to L^- and another version in which these rates are the same. The results (AIC weights comparison; Supplementary Table 4) point to the former model being preferred. The estimated rate to shift from L^- to L is 0.2865 and from L to L^- is 0.0106 per Myr.

For the longitudinal and latitudinal analyses, in addition to allowing different rates of diversification across elevational bands, we also allow the overall rate of diversification to differ between regions (that is tropical versus temperate regions, Old World versus New World). We did so by multiplying the rates in one region by a constant factor to give rates in the other region, and this factor was optimized. To avoid models with many parameters we did not consider the more complex scenario in which the elevation dependence in rates of diversification varies between regions. We assumed that the transition of species between regions (region exchange) happens to and from the same elevational band (low, mid and high only). While we assume that the transition rates between regions is the same for all elevational bands, these rates are different from the rates of transition between elevational bands within regions.

To prevent finding only local optima during the likelihood optimization, we used five different initial parameter sets. The first set of parameters were

the estimates of speciation and extinction from a birth–death model fit to the branching times and with transition rates assumed to be a fifth of speciation rate. For the second set, we doubled the speciation rates of the first set, and halved the transition rates. In the third, we halved the speciation rates of the first set and doubled the transition rates. Similarly, the fourth had doubled extinction rates and halved transition rates, and the fifth had halved extinction rates and doubled transition rates compared to the first set. The highest likelihood of the five starting points was taken as the global optimum and used to compare across models. We used AIC weights—thus penalizing the number of free parameters—to select the best models per analysis.

Our global, latitudinal and longitudinal analyses differ in their assumptions of the factors that influence diversification rates (elevation only; elevation and latitude; elevation and longitude). Using only the data necessary to study these dependencies would prevent model comparison, because the datasets would differ. We had 6 states in the global analysis (as there are 6 elevational bands), whereas the longitudinal analysis has 12 states (6 bands in combination with tropical and temperate regions) that are different from the 12 states in latitudinal analysis (6 bands in combination with New and Old Worlds). Therefore, we made the AIC values comparable by adding an extra likelihood term to the likelihood computed by SecSSE that covers the transitions not covered in SecSSE, using the function `fitDiscrete` from the R package 'geiger'⁵³. That is, for the longitudinal analysis we added the (maximum) log likelihood of a simple model of transitions in latitude that uses the phylogenetic tree. In this way, the total likelihood of the longitudinal analysis incorporates the likelihood of a model with transitions across elevations and longitude (computed by SecSSE) and a model of transitions between latitudes (computed by geiger). Note that only the component calculated using SecSSE handles diversification rates and state transitions simultaneously. Similarly, for the latitudinal analysis we added the (maximum) log likelihood of a model of transitions in longitude given the phylogenetic tree, and for the global analysis we added the (maximum) log likelihood of a model of transitions in both longitude and latitude—which in fact is the sum of the two previous log likelihoods.

Finally, to provide a more direct comparison with previous studies, we also examined the association between elevation and tip-DR using ANOVA and a phylogenetic generalized linear model fitted in the R package 'caper'. For our predictor variable we assigned species as either 'highland' (high, mid–high) or 'lowland' (low, low–mid) and excluded species limited to mid-elevations (mid) or spanning the entire gradient (full range), resulting in $n = 5,186$ species. We calculated tip-DR using the 'evol_distinct' function of the 'phyloregion' R package⁵⁴.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

No datasets were generated during the current study. The data analysed were collected from previous reports^{27,49}. The necessary files to replicate our study are available at figshare: <https://doi.org/10.6084/m9.figshare.14750652>.

Code availability

We used R packages for analysing data. They are all available at CRAN: caper, phyloregion, DDD and secsse. The R code that we used to set up models, import data and analyse the output is available at figshare: <https://doi.org/10.6084/m9.figshare.14750652>.

Received: 14 October 2020; Accepted: 16 June 2021;

Published online: 22 July 2021

References

- Lomolino, M. V. Elevation gradients of species-density: historical and prospective views. *Glob. Ecol. Biogeogr.* **10**, 3–13 (2001).
- McCain, C. M. Global analysis of reptile elevational diversity. *Glob. Ecol. Biogeogr.* **19**, 541–553 (2010).
- Quintero, I. & Jetz, W. Global elevational diversity and diversification of birds. *Nature* **555**, 246–250 (2018).
- Orme, C. D. L. et al. Global hotspots of species richness are not congruent with endemism or threat. *Nature* **436**, 1016–1019 (2005).
- Rahbek, C. et al. Humboldt's enigma: what causes global patterns of mountain biodiversity? *Science* **365**, 1108–1113 (2019).
- Wiens, J. J., Parra-Olea, G., García-París, M. & Wake, D. B. Phylogenetic history underlies elevational biodiversity patterns in tropical salamanders. *Proc. R. Soc. B* **274**, 919–928 (2007).
- Pigot, A. L., Trisos, C. H. & Tobias, J. A. Functional traits reveal the expansion and packing of ecological niche space underlying an elevational diversity gradient in passerine birds. *Proc. R. Soc. B* **283**, 20152013 (2016).
- Körner, C. & Spehn, E. M. (eds) *Mountain Biodiversity: A Global Assessment* (CRC Press, 2002).
- Merckx, V. S. F. T. et al. Evolution of endemism on a young tropical mountain. *Nature* **524**, 347–350 (2015).
- Fjeldsø, J. Geographical patterns for relict and young species of birds in Africa and South America and implications for conservation priorities. *Biodivers. Conserv.* **3**, 207–226 (1994).
- Jetz, W., Rahbek, C. & Colwell, R. K. The coincidence of rarity and richness and the potential signature of history in centres of endemism. *Ecol. Lett.* **7**, 1180–1191 (2004).
- Weir, J. T. Divergent timing and patterns of species accumulation in lowland and highland Neotropical birds. *Evolution* **60**, 842–855 (2006).
- Hughes, C. & Eastwood, R. Island radiation on a continental scale: exceptional rates of plant diversification after uplift of the Andes. *Proc. Natl Acad. Sci. USA* **103**, 10334–10339 (2006).
- Cozzarolo, C.-S. et al. Biogeography and ecological diversification of a mayfly clade in New Guinea. *Front. Ecol. Evol.* **7**, 233 (2019).
- Davies, T. J., Savolainen, V., Chase, M. W., Moat, J. & Barraclough, T. G. Environmental energy and evolutionary rates in flowering plants. *Proc. R. Soc. B* **271**, 2195–2200 (2004).
- Graves, G. R. Linearity of geographic range and its possible effect on the population structure of andean birds. *Auk* **105**, 47–52 (1988).
- Janzen, D. H. Why mountain passes are higher in the tropics. *Am. Nat.* **101**, 233–249 (1967).
- Cai, T. et al. What makes the Sino-Himalayan mountains the major diversity hotspots for pheasants? *J. Biogeogr.* **45**, 640–651 (2018).
- Rana, S. K., Gross, K. & Price, T. D. Drivers of elevational richness peaks, evaluated for trees in the east Himalaya. *Ecology* **100**, e02548 (2019).
- Rahbek, C. et al. Building mountain biodiversity: geological and evolutionary processes. *Science* **365**, 1114–1119 (2019).
- Ribas, C. C., Moyle, R. G., Miyaki, C. Y. & Cracraft, J. The assembly of montane biotas: linking Andean tectonics and climatic oscillations to independent regimes of diversification in Pionus parrots. *Proc. R. Soc. B* **274**, 2399–2408 (2007).
- Schwery, O. et al. As old as the mountains: the radiations of the Ericaceae. *N. Phytologist* **207**, 355–367 (2015).
- Bates, J. M. & Zink, R. M. Evolution into the Andes: molecular evidence for species relationships in the genus *Leptopogon*. *Auk* **111**, 507–515 (1994).
- Roy, M. S. Recent diversification in African greenbul (Pycnonotidae: *Andropadus*) supports a montane speciation model. *Proc. R. Soc. B* **264**, 1337–1344 (1997).
- García-Moreno, J. et al. Pre-Pleistocene differentiation among chat-tyrants. *Condor* **100**, 629–640 (1998).
- Oliveros, C. H. et al. Earth history and the passerine superradiation. *Proc. Natl Acad. Sci. USA* **116**, 7916–7925 (2019).
- Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K. & Moores, A. O. The global diversity of birds in space and time. *Nature* **491**, 444–448 (2012).
- Title, P. O. & Rabosky, D. L. Tip rates, phylogenies and diversification: what are we estimating, and how good are the estimates? *Methods Ecol. Evol.* **10**, 821–834 (2019).
- Herrera-Alsina, L., van Els, P. & Etienne, R. S. Detecting the dependence of diversification on multiple traits from phylogenetic trees and trait data. *Syst. Biol.* **68**, 317–328 (2019).
- Weir, J. T. & Schluter, D. The latitudinal gradient in recent speciation and extinction rates of birds and mammals. *Science* **315**, 1574–1576 (2007).
- Derryberry, E. P. et al. Lineage diversification and morphological evolution in a large-scale continental radiation: the Neotropical ovenbirds and woodcreepers (Aves: Furnariidae). *Evolution* **65**, 2973–2986 (2011).
- Fjeldsø, J., Bowie, R. C. K. & Rahbek, C. The role of mountain ranges in the diversification of birds. *Annu. Rev. Ecol. Syst.* **43**, 249–265 (2012).
- Chazot, N. et al. Into the Andes: multiple independent colonizations drive montane diversity in the Neotropical clearwing butterflies Godyrina. *Mol. Ecol.* **25**, 5765–5784 (2016).
- Elias, M. et al. Out of the Andes: oatterns of diversification in clearwing butterflies. *Mol. Ecol.* **18**, 1716–1729 (2009).
- McGuire, J. A., Witt, C. C., Altshuler, D. L. & Remsen, J. V. Phylogenetic systematics and biogeography of hummingbirds: Bayesian and maximum likelihood analyses of partitioned data and selection of an appropriate partitioning strategy. *Syst. Biol.* **56**, 837–856 (2007).
- Brumfield, R. T. & Edwards, S. V. Evolution into and out of the Andes: a Bayesian analysis of historical diversification in *Thamnophilus* antshrikes. *Evolution* **61**, 346–367 (2007).
- Zhou, C. et al. Genome-wide analysis sheds light on the high-altitude adaptation of the buff-throated partridge (*Tetraophasis szechenyii*). *Mol. Genet. Genom.* **295**, 31–46 (2020).
- Xu, Z., He, J. & Wang, J. Hypoxia affects the resistance of *Scylla paramamosain* to *Vibrio alginolyticus* via changes of energy metabolism. *Aquac. Rep.* **19**, 100565 (2021).
- Storz, J. F., Scott, G. R. & Cheviron, Z. A. Phenotypic plasticity and genetic adaptation to high-altitude hypoxia in vertebrates. *J. Exp. Biol.* **213**, 4125–4136 (2010).
- Scott, G. R. Elevated performance: the unique physiology of birds that fly at high altitudes. *J. Exp. Biol.* **214**, 2455–2462 (2011).

41. Projecto-García, J. et al. Repeated elevational transitions in hemoglobin function during the evolution of Andean hummingbirds. *Proc. Natl Acad. Sci. USA* **110**, 20669–20674 (2013).
42. Scott, G. R. et al. Molecular evolution of cytochrome C oxidase underlies high-altitude adaptation in the bar-headed goose. *Mol. Biol. Evol.* **28**, 351–363 (2011).
43. Schumm, M., White, A. E., Supriya, K. & Price, T. D. Ecological limits as the driver of bird species richness patterns along the east Himalayan elevational gradient. *Am. Nat.* **195**, 802–817 (2020).
44. Malpica, A., Covarrubias, S., Villegas-Patraca, R. & Herrera-Alsina, L. Ecomorphological structure of avian communities changes upon arrival of wintering species. *Basic Appl. Ecol.* **24**, 60–67 (2017).
45. Etienne, R. S. et al. A minimal model for the latitudinal diversity gradient suggests a dominant role for ecological limits. *Am. Nat.* **194**, E122–E133 (2019).
46. Freeman, B. G., Scholer, M. N., Ruiz-Gutierrez, V. & Fitzpatrick, J. W. Climate change causes upslope shifts and mountaintop extirpations in a tropical bird community. *Proc. Natl Acad. Sci. USA* **115**, 11982–11987 (2018).
47. Bouckaert, R. et al. BEAST 2: a software platform for Bayesian evolutionary analysis. *PLoS Comput. Biol.* **10**, e1003537 (2014).
48. Braun, E. L., Cracraft, J. & Houde, P. in *Avian Genomics in Ecology and Evolution* (ed. Kraus, R. H. S.) 151–210 (Springer, 2019).
49. del Hoyo, J., Elliott, A., Sargatal, J., Christie, D. A. & Kirwan, G. *Handbook of the Birds of the World* (Lynx Edicions, 2016).
50. Chapman, F. M. et al. The distribution of bird life in Ecuador: a contribution to a study of the origin of Andean bird-life. *Bull. Am. Mus. Nat. Hist.* **55**, 1–784 (1926).
51. Maddison, W. P., Midford, P. E. & Otto, S. P. Estimating a binary character's effect on speciation and extinction. *Syst. Biol.* **56**, 701–710 (2007).
52. Beaulieu, J. M. & O'Meara, B. C. Detecting hidden diversification shifts in models of trait-dependent speciation and extinction. *Syst. Biol.* **65**, 583–601 (2016).
53. Harmon, L. J., Weir, J. T., Brock, C. D., Glor, R. E. & Challenger, W. GEIGER: investigating evolutionary radiations. *Bioinformatics* **24**, 129–131 (2008).
54. Daru, B., Karunarathne, P. & Schliep, K. phyloregion: R package for biogeographic regionalization and spatial conservation. *Methods Ecol. Evol.* **11**, 1483–1491 (2020).

Acknowledgements

The research of P.v.E. was facilitated by the Adaptive Life Program of the Groningen Institute for Evolutionary Life Sciences, Faculty of Science and Engineering at the University of Groningen. L.H.-A. thanks the Consejo Nacional de Ciencia y Tecnología of Mexico for funding (CVU 385304 L). R.S.E. thanks the Netherlands Organization for Scientific Research (NWO) for financial support through a VICI grant. A.L.P. is funded by a Royal Society University Research Fellowship. We thank the Center for Information Technology of the University of Groningen for their support and for providing access to the Peregrine high-performance computing cluster.

Author contributions

P.v.E. collected data. L.H.-A. and P.v.E. performed the analysis. R.S.E. and A.L.P. supervised the project. L.H.-A., P.v.E., A.L.P. and R.S.E. wrote the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information The online version contains supplementary material available at <https://doi.org/10.1038/s41559-021-01515-y>.

Correspondence and requests for materials should be addressed to L.H.-A.

Peer review information *Nature Ecology & Evolution* thanks the anonymous reviewers for their contribution to the peer review of this work. Peer reviewer reports are available.

Reprints and permissions information is available at www.nature.com/reprints.

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

© The Author(s), under exclusive licence to Springer Nature Limited 2021

Reporting Summary

Nature Portfolio wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Portfolio policies, see our [Editorial Policies](#) and the [Editorial Policy Checklist](#).

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a Confirmed

- ☐ ☒ The exact sample size (n) for each experimental group/condition, given as a discrete number and unit of measurement
- ☐ ☒ A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
- ☐ ☒ The statistical test(s) used AND whether they are one- or two-sided
Only common tests should be described solely by name; describe more complex techniques in the Methods section.
- ☐ ☒ A description of all covariates tested
- ☐ ☒ A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
- ☐ ☒ A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
- ☒ ☐ For null hypothesis testing, the test statistic (e.g. F , t , r) with confidence intervals, effect sizes, degrees of freedom and P value noted
Give P values as exact values whenever suitable.
- ☒ ☐ For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
- ☐ ☒ For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
- ☒ ☐ Estimates of effect sizes (e.g. Cohen's d , Pearson's r), indicating how they were calculated

Our web collection on [statistics for biologists](#) contains articles on many of the points above.

Software and code

Policy information about [availability of computer code](#)

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

Data analysis We used R packages for analyzing data. They are all available at CRAN: caper, phyloregion, DDD and secsse

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors and reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Portfolio [guidelines for submitting code & software](#) for further information.

Data

Policy information about [availability of data](#)

All manuscripts must include a [data availability statement](#). This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A description of any restrictions on data availability
- For clinical datasets or third party data, please ensure that the statement adheres to our [policy](#)

No datasets were generated during the current study. Data analyzed was collected from del Hoyo et al (2016): Handbook of the Birds of the World Alive and from Jetz et al (2012): The global diversity of birds in space and time. Nature 491:444–448.
The necessary files to replicate our study are available at Figshare: 10.6084/m9.figshare.14750652.

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see [nature.com/documents/nr-reporting-summary-flat.pdf](https://www.nature.com/documents/nr-reporting-summary-flat.pdf)

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We use a phylogenetic diversification model that accounts for the dispersal of species across elevations to examine the evolutionary dynamics of the elevational diversity gradient in passerine birds
Research sample	The entire passerine clade
Sampling strategy	The entire passerine clade
Data collection	PvE collected elevation data from del Hoyo et al (2016): Handbook of the Birds of the World Alive and from Jetz et al (2012): The global diversity of birds in space and time. Nature 491:444–448.
Timing and spatial scale	Global spatial scale over evolutionary time
Data exclusions	We did not include occasional records at extreme elevation. Elevational distributions are based on the breeding range, thus excluding wintering and transient elevation records
Reproducibility	Our analysis can be replicated, we provide code for this
Randomization	Because the global nature of our analysis, species were not selected randomly
Blinding	We used information that had already been published, so no blinding was needed
Did the study involve field work?	☐ Yes ☒ No

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☒	☐ Palaeontology and archaeology
☒	☐ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data
☒	☐ Dual use research of concern

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging