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Disentangling the historical routes to community assembly in the global epicentre of biodiversity

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Abstract

Understanding the processes through which ecological communities are assembled remains a major challenge, particularly in hotspots of biodiversity such as tropical mountains. Here, we apply continuous-time Markov models to elevational, geographical and phylogenetic data for 166 avian sister pairs to infer the relative frequency of different historical pathways involved in the build-up of species on Neotropical mountains, the Earth's most biodiverse terrestrial region. We show that sister species arising in geographic isolation but now sympatric (i.e. living on the same mountain slope), have assembled through a mix of different routes. Ecological sorting whereby species diverge to different elevations in allopatry occurs with a similar frequency to ecological displacement where divergence in elevation occurs upon secondary contact. However, both these routes are far less common than ecological niche conservatism, whereby species transition to sympatry without diverging in their elevation range. Our results suggest the predominance of this more direct and thus faster route to sympatry may help explain the exceptional species richness of tropical mountains.

Keywords: biotic interactions, elevational range, character displacement, sympatry, species sorting, community assembly

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1. Introduction

Explaining the combination and diversity of species that co-occur within communities remains a major challenge in ecology. This is in part because the patterns of spatial overlap observed at the present depend not only on current ecological interactions between species, but also on historical processes that play out over much longer time-frames and that are beyond the reach of direct observation or experimental manipulation [1,2]. These historical processes include speciation, niche evolution, dispersal, and range expansions [3–5], with differences in the dynamics of these processes and the ecological factors controlling them, underlying different theoretical models for how communities are assembled.

One of the main models for how communities assemble is based on the idea that new species arising in spatial isolation (i.e. allopatry) diverge in their ecological niche, and only those that happen to diverge sufficiently to minimise competition are able to co-occur when they come back into secondary contact [6,7]. According to this model, community assembly largely involves the 'ecological sorting' of pre-existing variation arising due to geographically variable selection pressures. An alternative to the ecological sorting model, proposes that niche differences between co-occurring species arise upon secondary contact, with competition between species driving divergent selection and a displacement of their ecological niches [8]. As with 'ecological sorting', this 'ecological displacement' (termed 'character displacement' when considering heritable traits) model assumes that niche similarity limits co-occurrence, but differs in its predictions of when and why niche differences evolve. A final possibility, is that species may re-assemble into communities whilst retaining their ancestral niche. This 'niche conservatism' model [9] is expected to predominate if ecological niche overlap is not limiting, either because of other constraints on co-occurrence (e.g. dispersal limitation) or because species have diverged along alternative niche dimensions [10].

A classic system for studying these historical processes concerns the distribution of vertebrates on mountains in the tropics. Tropical mountains are renowned for their exceptional diversity. For instance, in the tropical Andes over 1000 species of birds can be found living on a single mountain slope [11]. Since most speciation events involve the geographic isolation of populations on different mountains (i.e. allopatry) [12–14], the main problem is to understand how these species subsequently assemble on the same mountain slope (i.e. sympatry) and partition ecological niche space. In this case, sympatry may involve species co-occurring at the same elevation. However, elevation can also be regarded as a key niche axis along which species can diverge and thus coexist at the scale of the entire mountain slope. Indeed, many species have very narrow elevation distributions (e.g. a few

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hundred metres in vertical distance) and replace one another across the gradient [15,16]. Previous studies have variously provided evidence that niche conservatism, ecological sorting and displacement may all be involved in shaping these patterns of co-occurrence and turnover along mountain slopes, but progress in disentangling their relative contributions has been limited.

One problem is that different assembly models can lead to same present day pattern. In particular, according to the niche conservatism model, species living on the same mountain slope have overlapping elevation ranges because they retain the adaptations to specific environmental conditions inherited from their ancestor [9]. However, while some studies have argued that niche conservatism is a pervasive process [17], the same pattern could also arise under the ecological displacement model. In this case, competition on secondary contact first forces species to occupy different elevations, but as species diverge along alternative niches dimensions (e.g. resource or microhabitat use) they subsequently expand their elevation ranges and overlap along the gradient. This ecological displacement model has also been proposed to be the dominant process explaining the build-up of co-occurring species on tropical mountains [3,16].

A similar challenge exists when trying to discriminate ecological sorting and displacement. Both these models predict that species living on the same mountain slope should have non-overlapping elevation ranges, at least prior to any subsequent niche expansion. Thus, discriminating between these scenarios depends critically on inferences about whether elevational divergence precedes or is coincident with the attainment of secondary contact. Studies attempting to address this issue have variously used phylogenetic information to infer the relative timing of niche divergence and secondary sympatry or have compared elevation divergence between sister species in zones of sympatry to places where they remain allopatric [8,18]. However, while such tests can potentially detect evidence of whether a particular process operates or not, critically they do not reveal how frequently this process occurs and thus its relative contribution to the build-up of sympatric diversity [19]. Progress in understanding community assembly, thus requires new approaches that can reliably infer the relative frequencies of different historical processes underlying current patterns of species distributions.

Here, we investigate the relative frequency of ecological displacement, sorting, and niche conservatism and how they contribute to the co-occurrence of passerine birds across elevation gradients in the Neotropics. We first constructed a new dataset consisting of the divergence time, geographical and elevational distribution of n = 166 sister species. We then apply a novel modelling approach that builds on previous studies examining the transition to

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sympatry using continuous-time Markov models [10], but extend this framework by considering the multiple routes through which species can attain sympatry via the evolution of elevational ranges. Focussing on avian sister species, where we can confidently assume that speciation involves the geographic isolation of populations [12,20], allows us to use information on the current age and state (e.g. allopatric or sympatric, and overlapping in elevation or not) to model the historical pathways through which co-occurrence arises. Using this approach, we address three main objectives. First, what is relative importance of ecological sorting, displacement and niche conservatism in build-up of sympatry among Neotropical montane sister species? Second, what is the relative importance of ecological sorting and displacement in generating turnover between sister species across elevation gradients and how does co-occurrence at the same elevation arise? Third, can our framework accurately and precisely infer the rate at which species pairs pass through these different historical routes?

2. Material and methods

(a) Elevational and geographic data

We compiled a dataset consisting of avian sister species occurring in the tropical mountain ranges of the Neotropics. Sister species and their respective divergence times were extracted from two recently published phylogenies covering respectively >95% and >98% of the New World oscines and suboscines [21,22]. We only kept sister pairs that met the following conditions: (1) At least one of the species occupies montane habitat, defined as areas >500m above sea-level [3]. (2) Both species occupy predominantly humid environments such that species pairs could realistically live on the same mountain slope, e.g. we removed species pairs if one sister occupied predominantly arid habitat, assessed with information from field guides. (3) Both species live in the Neotropics, which included the tropical mountain ranges of Central-America. Species that had ranges stretching into North-America were included in the dataset if they were primarily Neotropical. The final dataset consisted of n = 166 sister pairs. To establish that our results were robust and to verify previously published results, we also reanalysed a previously published global dataset of montane sister species (Supplementary material, Figure S2)[3].

We scored whether each sister pair was allopatric or sympatric and whether they had overlapping or non-overlapping elevational distribution. Geographical and elevational range data was gathered primarily from regional field guides [23–27] and supplemented by *Birds of the World (BW)* [28]. *BW* typically reflects information found in local field guides but incorporates more recent taxonomic changes. Sympatry was defined as when sister species were present on the same mountain slope, regardless of whether this overlap was

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widespread (i.e. thousands of kms) or minimal (i.e. a few kms). In contrast, allopatry was defined as when sister species occurred exclusively on different mountain summits or regions, often separated by obvious geographical barriers (e.g. valleys).

We assigned species pairs to one of five possible discrete states, defined by the combination of sympatry/allopatry and elevation overlap/non-overlap. For sister species occurring in allopatry, they may have overlapping (state 1) or non-overlapping (state 3) elevational ranges. To ensure our results were not biased by marginal overlap along narrow contact zones, we used a threshold of elevation overlap of 20%, calculated as a proportion of the species with the narrower elevation range. To test the robustness of our conclusions, however, we also repeated our analysis using different values (1, 10, and 30% overlap, Figure S1).

Sister species occurring in sympatry may have non-overlapping elevational ranges (state 4), overlapping elevational ranges (state 5), or elevational ranges that overlap in allopatry but not sympatry (state 2). Assignment to state 2 can only be done if sister species occur partially in sympatry but at least one sister has a partially allopatric distribution, and no other closely related species forms a hypothesised elevational replacement in the allopatric part of their range. The latter condition was to ensure that any intraspecific variation was not caused by a tertiary species, as this would not be the result of interactions between the sister species. We assessed this with observations mentioned in field guides combined with any information on geographic and elevational ranges of congeners.

(b) Statistical analysis using Markov models

To infer the relative importance of different assembly scenarios in explaining the build-up of sympatry we developed a continuous time multi-state Markov model (Figure 1). In this model, the initial state for sister species is allopatry with overlapping elevational ranges (state 1), which reflects the situation expected at the time of their initial divergence [29]. Sister pairs then stochastically transition between states, with different transition pathways corresponding to the different assembly scenarios. Under the ecological sorting scenario, sister species first transition to having non-overlapping elevation ranges whilst remaining in allopatry (state 3). They can subsequently transition to having non-overlapping elevation ranges and occurring in sympatry (state 4). Under the ecological displacement scenario, sister species instead transition from state 1 to having non-overlapping elevation ranges in sympatry but maintaining overlapping elevation ranges in allopatry (state 2). Finally, the niche conservatism scenario is described by a direct transition from state 1 to sympatry and overlapping elevational ranges (state 5).

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Once sympatry between sister species is attained (states 2, 4 or 5) we allow the further evolution of species elevational ranges. Sister pairs in state 2 (i.e. elevation overlap in allopatry and non-overlap in sympatry), can subsequently diverge in their elevation range in the allopatric part of their distribution (e.g. due to ecological opportunity) and thus transition to state 4. Alternatively, they can converge in their elevation range in their sympatric distribution (e.g. due to differentiation along an alternative niche axis reducing competition) and thus transition to state 5. Equally, we allow the possibility that sympatric sister species with non-overlapping elevation ranges (state 4) may subsequently converge to occur at the same elevation (state 5) [4,30]. Our model thus allows for the overlap (state 5) of sister pairs on the same mountain slope, which is considered to be the final state, to be attained through any of the three community assembly scenarios

Based on the estimated time since divergence and states of sister pairs at present we used maximum likelihood (ML) [31] to estimate the transition rates between the states. The full model contains 7 rate parameters corresponding to the 7 possible state transitions. We also considered simpler models by, for instance, constraining the transition rate from state 1 to 2 to be equivalent to the transition rate from state 2 to 3. The simplest model has only a single rate parameter, corresponding to identical rates for all transitions. We compared model fit across all (n = 877) combinations according to AIC and report both the best model and the model averaged parameter values of all highly supported models (ΔAIC ≤ 2 of best model).

(c) Relative frequency of trajectories

Having inferred the transition rates between states, we used these to estimate the relative contribution of ecological displacement (ED), ecological sorting (ES), and niche conservatism (NC) in the build-up of sympatry. Specifically, we used the inferred rates to perform 1000 posterior predictive simulations using the Gillespie algorithm for constant rates [32]. Under the Gillespie algorithm, transitions between states correspond to events. The simulation starts at time $t = 0$, indicating the time since divergence for all sister species. The waiting time (δ) to the next event is determined by a random draw from an exponential distribution with the mean equal to the sum of all transition rates across all sister pairs, e.g. if the transition rate from state 1 to 2 (r12) is 0.05 and there are currently 5 pairs in state 1, then this transition adds 0.25 to the total rate. The event that occurs at time $t + \delta$ is selected with a probability equal to the relative contribution of each rate to the total rate. This transition applies to a single species pair and this pair is chosen at random with equal weighting across all pairs that are currently in the relevant state. As we simulate forward in time, species can no longer transition if they are younger than t. The simulation is initiated with all sister pairs

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being in state 1 and terminated once time *t* is greater than the age of the oldest sister pair. During the simulation we record the percentage of sister pairs passing through each of the three pathways corresponding to different community assembly scenarios (i.e. ED, ES, and NC), and report the mean and standard deviation across simulations runs.

(d) Assessing model fit

Although the model is optimised using maximum likelihood, model fit may be poor if the underlying assumptions of the model are not met. If that is the case, estimated rates will poorly reflect the empirical observations. We assessed how well the predicted transition rates can predict the distribution of states among the sister pairs using the output of the posterior predictive simulations. To examine if there is bias in the effectiveness of our model depending on species age, we bin species pairs in three equal-width age bins: 0.07-3.80, 3.80-7.52, and 7.52-11.25 million years (Myr), where 0.07 and 11.25 Myr are the age of the youngest and oldest pair. We used three bins to ensure we would approximately capture any changes in the trend in the prevalence of states through time beyond increases and decreases. The prevalence of each of the five states per age bin is then compared between the empirical data and 95% confidence intervals constructed from the final prevalence of the simulated states. If the empirical prevalence falls within the confidence intervals this would indicate good model fit (Figure 3), but large CI's would likewise indicate high uncertainty.

(e) Simulation tests of accuracy and precision

Using simulations, we further evaluate the model by assessing if we can both accurately and precisely recover the transition rates. High accuracy indicates that the model is not biased towards over- or under-estimating particular transition rates. High precision indicates that the estimated rates are close to the true rates. We explored a number of different scenarios, designed to characterise the three different assembly models and variants of these (S1-S3), as well as a scenario assuming identical transition rates (S4) and one corresponding to the transition rates inferred from the empirical data (S5). For each scenario, we performed 100 replicate simulations using the observed number and ages of sister pairs. For each simulation, we then performed an identical model fitting procedure as for our empirical data, reporting the parameter estimate for both the best model and the model averaged rates. We evaluate the accuracy and precision of the rate estimates using the median and 95% confidence intervals of the estimated rates.

3. Results

(a) Empirical distribution of sister pair states

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Across the *n* = 166 sister species pairs, the majority are currently in allopatry with overlapping elevation ranges (state 1: 62%). The next most common state is sympatry with overlapping elevation ranges (state 5: 21%), with fewer pairs having non-overlapping elevational ranges and occurring in sympatry (state 4: 7%), or allopatry (state 3: 5%) or having non-overlapping elevational ranges in sympatry but overlapping elevational ranges in allopatry (state 2: 5%). The mean age of pairs that are in allopatry with overlapping elevation ranges (state 1: 2.31Myr) is younger than all other states (state 2: 3.46, state 3: 3.19, state 4: 3.95, and state 5: 3.44Myr), consistent with our assumption that is the initial state at the time of species divergence.

(b) Transition rates between states

We found that our best model contains three parameters and constrains r12, r13, r25, and r45 to 0.04 (CI95: 0.03-0.07), r15 to 0.10 (CI95: 0.07-0.14), and r24, r34 to 0.33 (CI95: 0.17-0.63). While there are 41 models that are highly supported (<2 ΔAIC), the model-averaged rate estimates are very similar to the best model. Because of this, we focus on the model-averaged results below. The model averaged results show that the transition rate from a state of allopatry with overlapping elevation ranges (state 1) to non-overlapping elevation ranges, either while in allopatry (r13 = 0.05/Myr) or upon the attainment of sympatry (r12 = 0.04/Myr) is relatively slow. In contrast, the transition rate of allopatric pairs with overlapping elevation ranges (state 1) to sympatry with overlapping elevation ranges (state 5) is significantly faster (r15 = 0.10/Myr).

(c) Accuracy and reliability of estimated transition rates

Our simulations show that transition rates from state 1 (r12, r13, and r15) (Figure 1), can be reliably and accurately estimated irrespective of the simulated scenario (Table 1). Later transitions (r24, r25, r34, r45) are estimated with less accuracy, probably because there are relatively few old sister pairs and thus less information to reliably estimate these rates. However, this does not affect the reliability of our conclusions because our aim is to infer the proportion of species pairs that embark on the different historical routes to sympatry and this depends on accurate estimation of the initial rates from state 1.

(d) The relative contribution of community assembly routes

The posterior-predictive simulations show that following speciation a similar proportion of pairs embark on the ecological sorting (27.27%, CI95: 16.36-39.13%) and ecological displacement (20.63%, CI95: 11.11-30.44%) routes, whereby species diverge in elevation while in allopatry (i.e. from state 1 to state 3) or upon secondary contact (i.e. from state 1 to state 2) respectively (Figure 2b). Of the pairs with currently non-overlapping elevation ranges

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in sympatry (states 2 and 4), more are inferred to be generated through ecological displacement (58.82%, CI95: 35.00-80.02%) than sorting (41.18%, CI95: 19.98-65.00%) (Figure 2c). However, confidence intervals on the proportion of pairs estimated to undergo ecological displacement and sorting broadly overlap, suggesting there is little evidence that one route is more common than the other.

Following speciation, the majority of pairs follow the niche conservatism route (51.67%, CI95: 39.39-64.52%), transitioning directly to sympatry without diverging in their elevation range (i.e. from state 1 to state 5) (Figure 2b). Of the species pairs that attain overlapping elevation ranges in sympatry (state 5) almost all of these (93.94%, CI95: 83.87-100.0%) originate through the niche conservatism route (Figure 2d). This can be explained because of the low transition rates in the early stages of the ecological sorting (r13) and displacement (r12) routes and because species pairs taking these route must pass through a number of intermediate states to attain overlapping elevation ranges in sympatry. We note that relaxing our threshold at which we consider species to have overlapping elevation ranges resulted in qualitatively similar results (Figure S1).

(d) Assessing model fit

The posterior-predictive simulations under the estimated parameter values predict the incidence of the five states well (Figure 3). The simulations capture the main patterns, namely: an increase with age of sympatric pairs that have not diverged in elevation (state 5), a decrease in the pairs that have not diverged in elevation and are allopatric (state 1), and slight increases for pairs that are either in allopatry or sympatry but have diverged in elevation (state 2, 3 and 4). However, the simulations also show that our model has large confidence intervals. This is likely caused by the uneven age distribution of species pairs in our empirical dataset. While there are 131 pairs <3.80 Myr and 33 pairs 3.80-7.52 Myr, only 2 sister pairs exceed 7.52Myr.

4. Discussion

Multiple historical processes have been proposed to explain the combination and diversity of species within ecological communities. However, because previous studies have focused on static biogeographic patterns and treated ecological sorting, displacement and niche conservatism as alternative explanations, their relative contribution to community assembly has remained unknown. Through our analysis of the dynamics of sympatry and elevation overlap among Neotropical montane birds, we present three key findings. First, we show that the relative contributions of different historical assembly models can be reliably inferred given current phylogenetic and geographic data among sister species. Second, our results show that ecological sorting and displacement contribute almost equally to explaining the turnover

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of closely related bird species across elevation gradients in the Neotropics. Finally, we show that the build-up of sympatry (i.e. living on the same mountain slope) and the overlap of sister species along elevation gradients is almost entirely (>90%) explained by conservatism of species elevation niches, rejecting more complex scenarios requiring niche displacement followed by subsequent expansion.

The high diversity of tropical mountains is associated with a rapid turnover of species as ecologically similar species replace one another up the mountain. Previous studies of montane birds have concluded that ecological displacement rather than sorting is the dominant process explaining such elevational replacements [3,16]. This is because most sister pairs with divergent elevation ranges currently occur in sympatry rather than allopatry, potentially consistent with the idea that divergence happens upon secondary contact rather than during geographic isolation. However, our results suggest that the importance of ecological sorting has been underestimated. This is because species that diverged in their elevation ranges while in allopatry can subsequently transition to sympatry, thus reducing the apparent incidence of allopatric pairs with divergent elevational ranges. Our phylogenetic model accounts for these historical dynamics and shows that ecological sorting and displacement contribute approximately equally to explaining turnover among sister species across tropical elevation gradients.

While our analysis detects evidence of both ecological sorting and displacement, we find that niche conservatism is a much more frequent route to sympatry, accounted for ~68% of sister species living on the same mountain slope. Such a high frequency of niche conservatism may not seem surprising, given that previous studies focussed on the drivers of speciation have shown that most vertebrate sister species have overlapping elevation ranges [9]. However, a high frequency of elevation overlap among sister species is by itself inconclusive regarding the mode of community assembly because the same pattern can arise under the ecological displacement model if the initial constraints on elevational overlap weaken as species diverge across alternative niche axis (e.g. resource use). Our phylogenetic approach to modelling the dynamics of elevation range overlap, enables us to exclude this possibility. Indeed, we estimate that displacement and subsequent overlap in species elevational ranges contributes little (3.57%) to current patterns of co-occurrence along elevation slopes.

Our finding that niche conservatism is more common than ecological sorting or displacement does not suggest that competition or other negative species interactions are unimportant in the assembly of montane bird communities. Indeed, evidence that interspecific competition limits elevational ranges is widespread in birds [33–35]. Instead, we

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suggest that species attaining sympatry without diverging in their elevation range are likely to have diverged across alternative niche dimensions such as resource or microhabitat use. Such an explanation would be consistent with previous evidence that coexistence of Neotropical bird species following speciation is limited by rates of divergence in key trophic traits, such as beak size [10]. Given the relatively young age of many Neotropical montane radiations and that there is little evidence for a slowdown in the rates of diversification, it is possible that local niche space at any point along the elevational gradient remains far from saturated [36]. As alternative niche dimensions become increasingly densely packed, it is possible that ecological sorting and displacement may become increasingly important routes to sympatry as has been suggested for New Guinean songbirds [16].

It could be argued that the relatively low frequency of ecological sorting and displacement inferred by our models is a peculiarity of Neotropical birds and that the dynamics of community assembly in this region may differ from other tropical mountain systems that have different geographic configurations and histories of uplift. However, we note that we obtained very similar results when re-analysing a global dataset of avian sister species (albeit skewed towards the Neotropics)(Fig. S2), suggesting that our conclusions may apply across tropical mountain regions generally. Another possible critique of our approach, is that by focussing on sister species we have not detected ecological displacement or sorting occurring among more distantly related species. Indeed, species that form elevational replacements along mountain slopes are often not sisters [37–39]. However, this is also unlikely to explain our results because it is among young, ecologically similar species that competition and other negative species interactions are expected to be strongest.

The expansion of species ranges following speciation is an essential step not only in the build-up of sympatry but also in providing renewed opportunities for further rounds of geographic isolation and thus the generation of new species. Our results show that the rate of range expansions leading to sympatry are substantially accelerated by the capacity for species to occur on the same slope without having to first diverge in their elevation niche. Specifically, according to our models, the expected lag time to sympatry under the niche conservatism route (10.26Myr), is substantially shorter than the lag time for species passing through the ecological sorting or displacement routes combined (29.39Myr). Thus, in addition to the turnover of species across elevations, a key additional ingredient explaining the high diversity of tropical mountains is the capacity for species to coexist locally at the same elevation.

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Our model represents a simplification of the complex processes governing the assembly of montane biotas and is limited to explaining the patterns of sympatry and elevation overlap among sister species. However, to our knowledge this is the first study to quantify the relative frequency of ecological sorting, ecological displacement, and niche conservatism in shaping species elevational ranges. A key next step will be to test how these dynamics may vary across different mountain regions or taxa that vary in their ecology. Such a comparative approach may be necessary to uncover why ecological sorting and displacement appear to be relatively rare between the species where we expect them to be most common. Our model could also be applied to disentangle the dynamics of assembly across other ecological gradients and evolutionary radiations, such as the vertical layering of foraging niches among rainforest birds [40], perch height among Anolis lizards [41] or depth zonation in the Cichlid fish of East African rift lakes [42].

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References

1. Mittelbach GG, Schemske DW. 2015 Ecological and evolutionary perspectives on community assembly. *Trends Ecol. Evol.* **30**, 241–247. (doi:10.1016/j.tree.2015.02.008)

2. Weber MG, Wagner CE, Best RJ, Harmon LJ, Matthews B. 2017 Evolution in a Community Context: On Integrating Ecological Interactions and Macroevolution. *Trends Ecol. Evol.* **32**, 291–304. (doi:10.1016/j.tree.2017.01.003)

3. Freeman BG. 2015 Competitive Interactions upon Secondary Contact Drive Elevational Divergence in Tropical Birds. *Am. Nat.* **186**, 470–479. (doi:10.1086/682703)

4. Wiens JJ *et al.* 2010 Niche conservatism as an emerging principle in ecology and

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conservation biology. *Ecol. Lett.* **13**, 1310–1324. (doi:10.1111/j.1461-0248.2010.01515.x)

5. Cadena CD. 2007 Testing the role of interspecific competition in the evolutionary origin of elevational zonation: An example with buarremon brush-finches (aves, emberizidae) in the neotropical mountains. *Evolution (N. Y).* **61**, 1120–1136. (doi:10.1111/j.1558-5646.2007.00095.x)

6. Pfennig DW, Pfennig KS. 2010 Character displacement and the origins of diversity. *Am. Nat.* **176**. (doi:10.1086/657056)

7. Stuart YE, Losos JB. 2013 Ecological character displacement: Glass half full or half empty? *Trends Ecol. Evol.* **28**, 402–408. (doi:10.1016/j.tree.2013.02.014)

8. Brown WL, Wilson EO. 1956 Character displacement. *Syst. Zool.* **5**, 49–64. (doi:10.2307/2411924)

9. Cadena CD *et al.* 2011 Latitude, elevational climatic zonation and speciation in New World vertebrates. *Proc. R. Soc. B Biol. Sci.* **279**, 194–201. (doi:10.1098/rspb.2011.0720)

10. Pigot AL, Jetz W, Sheard C, Tobias JA. 2018 The macroecological dynamics of species coexistence in birds. *Nat. Ecol. Evol.* **2**, 1112–1119. (doi:10.1038/s41559-018-0572-9)

11. Walker B, Stotz DF, Pequeno T, Fitzpatrick JW. 2006 Birds of the Manu Biosphere Reserve. *Fieldiana Zool.* **110**, 23–49. (doi:10.3158/0015-0754(2006)110[23:botmbr]2.0.co;2)

12. Price T. 2008 *Speciation in birds*. Greenwood village, Colorado: Roberts and Co.

13. Cadena CD, Céspedes LN. 2019 Origin of elevational replacements in a clade of nearly flightless birds – most diversity in tropical mountains accumulates via secondary contact following allopatric speciation. *bioRxiv* , 635–659. (doi:10.1101/606558)

14. Linck E, Freeman BG, Dumbacher JP. 2020 Speciation and gene flow across an elevational gradient in New Guinea kingfishers. *J. Evol. Biol.* **33**, 1643–1652. (doi:10.1111/jeb.13698)

15. Terborgh J, Weske JS. 1975 The role of competition in the distribution of Andean birds. *Ecology* **56**, 1237-562–576. (doi:10.2307/1939177)

16. Diamond JM. 1973 Distributional ecology of New Guinea Birds. *Science (80-.).* **179**,

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759–769. (doi:10.1126/science.179.4075.759)

17. Linck EB, Freeman BG, Cadena CD, Ghalambor CK. 2021 Evolutionary conservatism will limit responses to climate change in the tropics. *Biol. Lett.* **17**. (doi:10.1098/rsbl.2021.0363)

18. Lack D. 1947 *Darwin's finches*. Cambridge University Press Cambridge.

19. Anderson SAS, Weir JT. 2021 Character displacement drives trait divergence in a continental fauna. *Proc. Natl. Acad. Sci. U. S. A.* **118**. (doi:10.1073/pnas.2021209118)

20. Phillimore, Orme, Thomas, Blackburn, Bennett, Gaston, Owens. 2008 Sympatric Speciation in Birds Is Rare: Insights from Range Data and Simulations. *Am. Nat.* **171**, 646. (doi:10.2307/30119664)

21. Barker K, Burns KJ, Klicka J, Lanyon SM, Lovette IJ. 2015 New insights into New World biogeography: An integrated view from the phylogeny of blackbirds, cardinals, sparrows, tanagers, warblers, and allies. *Auk* **132**, 333–348. (doi:10.1642/AUK-14-110.1)

22. Harvey MG *et al.* 2020 The evolution of a tropical biodiversity hotspot. *Science (80-.).* **370**, 1343–1348. (doi:10.1126/science.aaz6970)

23. Athanas N, Greenfield PJ. 2016 *Birds of western Ecuador: A photographic guide*. Princeton University Press.

24. Hilty SL. 2003 *Birds of venezuela*. 2nd edn. Princeton University Press.

25. Schulenberg TS, Stotz DF, Lane DF, O'Neill JP, Parker TA. 2007 *Birds of peru*. Princeton University Press.

26. Vallely AC, Dyer D. 2018 *Birds of Central America*. Princeton University Press.

27. Stotz DF, Fitzpatrick JW, Parker III TA, Moskovits DK. 1996 *Neotropical birds: ecology and conservation*. University of Chicago Press.

28. Billerman SM, Keeney BK, Rodewald PG, Schulenberg TS, editors. 2020 *Birds of the World*. Ithaca, NY, USA: Cornell Laboratory of Ornithology.

29. Coyne JA, Orr HA. 2004 *Speciation*. Sunderland, MA: Sinauer Associates, Inc.

30. Tobias JA, Cornwallis CK, Derryberry EP, Claramunt S, Brumfield RT, Seddon N. 2014 Species coexistence and the dynamics of phenotypic evolution in adaptive radiation. *Nature* **506**, 359–363. (doi:10.1038/nature12874)

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31. Jackson CH. 2011 Multi-state models for panel data: The msm package for R. *J. Stat. Softw.* **38**, 1–28. (doi:10.18637/jss.v038.i08)

32. Gillespie DT. 1977 Exact stochastic simulation of coupled chemical reactions. *J. Phys. Chem.* **81**, 2340–2361. (doi:10.1021/j100540a008)

33. Freeman BG, Class Freeman AM, Hochachka WM. 2016 Asymmetric interspecific aggression in New Guinean songbirds that replace one another along an elevational gradient. *Ibis (Lond. 1859).* **158**, 726–737. (doi:10.1111/ibi.12384)

34. Freeman BG, Tobias JA, Schluter D. 2019 Behavior influences range limits and patterns of coexistence across an elevational gradient in tropical birds. *Ecography (Cop.).* , 1–9. (doi:10.1111/ecog.04606)

35. Freeman BG, Montgomery G. 2016 Interspecific aggression by the Swainson's Thrush (Catharus ustulatus) may limit the distribution of the threatened Bicknell's Thrush (Catharus bicknelli) in the Adirondack Mountains . *Condor* **118**, 169–178. (doi:10.1650/condor-15-145.1)

36. Weir JT. 2006 Divergent Timing and Patterns of Species Accumulation in Lowland and Highland Neotropical Birds. *Evolution (N. Y).* **60**, 842. (doi:10.1554/05-272.1)

37. Caro LM, Caycedo-Rosales PC, Bowie RCK, Slabbekoorn H, Cadena CD. 2013 Ecological speciation along an elevational gradient in a tropical passerine bird? *J. Evol. Biol.* **26**, 357–374. (doi:10.1111/jeb.12055)

38. García-Moreno J, Fjeldså J. 1999 Chronology and mode of speciation in the Andean avifauna. *Isol. Vertebr. Communities Trop. Proc. 4th Int. Symp.* , 25–46.

39. Patton JL, Smith MF. 1992 mtDNA phylogeny of Andean mice: a test of diversification across ecological gradients. *Evolution (N. Y).* **46**, 174–183. (doi:10.1111/j.1558-5646.1992.tb01992.x)

40. MacArthur RH. 1958 Population Ecology of Some Warblers of Northeastern Coniferous Forests. *Ecology* **39**, 599–619. (doi:10.2307/1931600)

41. Lister BC. 1976 The Nature of Niche Expansion in West Indian Anolis Lizards I: Ecological Consequences of Reduced Competition. *Evolution (N. Y).* **30**, 659–676.

42. Rodríguez MA, Lewis WM. 1997 Structure of fish assemblages along environmental gradients in floodplain lakes of the Orinoco River. *Ecol. Monogr.* **67**, 109–128. (doi:10.1890/0012-9615(1997)067[0109:SOFAAE]2.0.CO;2)

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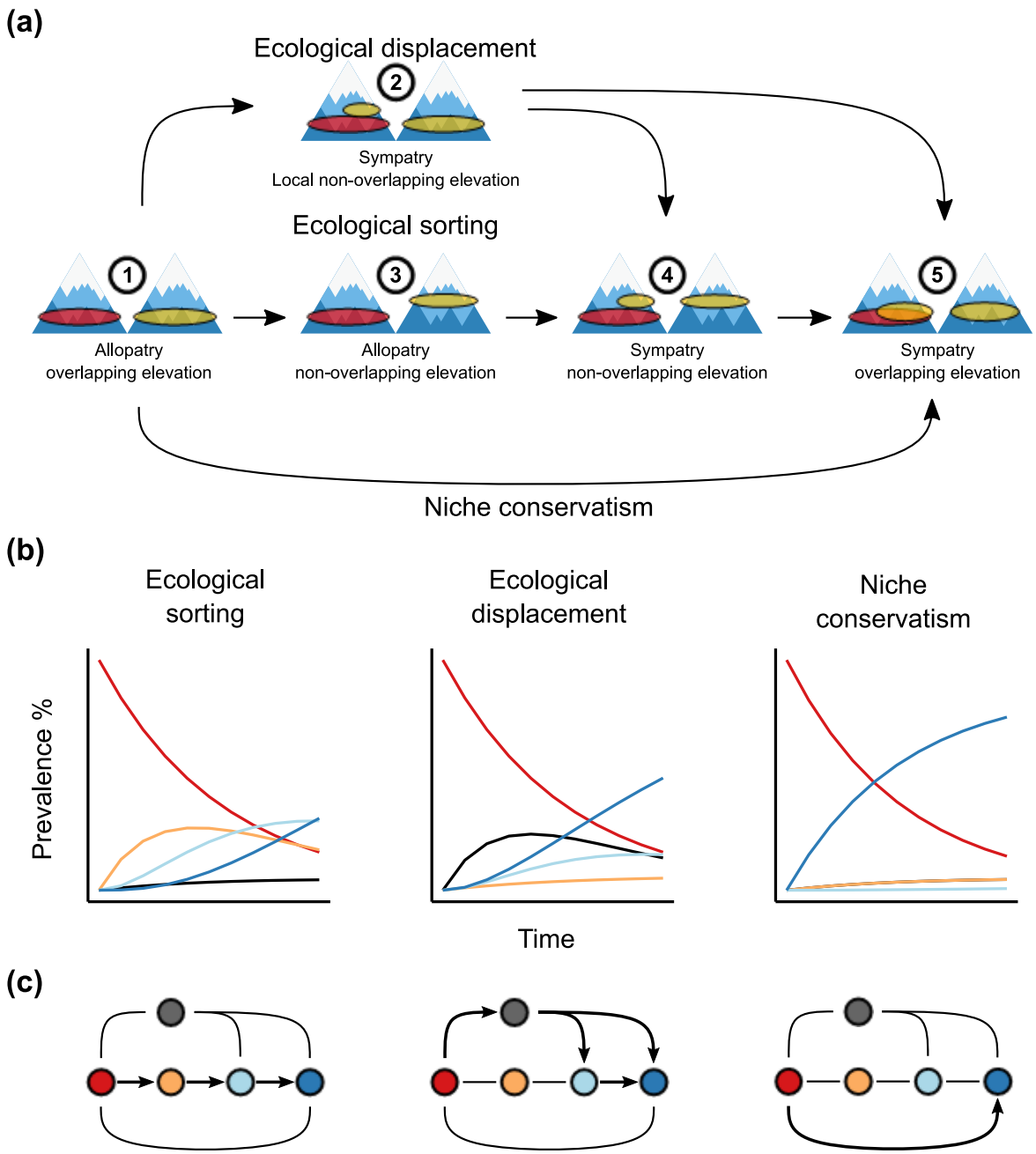

Figure 1 Hypothetical trajectories towards sympatry in montane sister species. a) All possible transitions in our models with their respective geographical and elevational context. (1) Species originate in allopatry and initially share the same elevational range. Subsequently, pairs might either stay in allopatry, but diverge in elevational range (3), attain partial elevational differentiation only in sympatry but retain overlap in allopatry (2), transition to sympatry but with differentiated elevational ranges (4), or transition to sympatry and co-occurrence (5). b) The prevalence of the five states through time according to the three hypothesised trajectories: I) Ecological sorting (ES), II) Ecological displacement (ED) and III) Niche conservatism (NC). These hypotheses are based on simulations in which the

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respective pathways are dominant highlight the differences in temporal dynamics. c) An abstract view of the dominant transitions under respectively ES, ED, and NC.

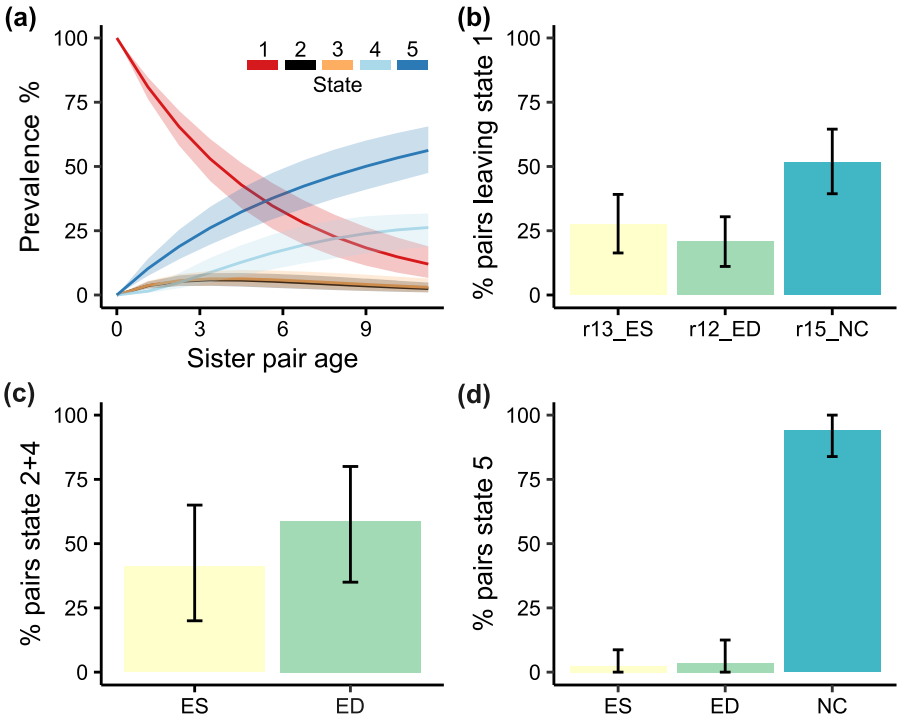

Figure 2 Sister species occurrence predictions through time and trajectories taken. a) predicted prevalence of the five states, as represented in Figure 1a, through time. State 2 and 3 overlap greatly in predicted prevalence. Shaded areas show 95% confidence intervals. b) Percentage of sister pairs that leave state 1 and start on each of the three routes towards sympatry. c) the percentage of pairs gone through either ecological sorting (ES) or ecological displacement (ED) that occupy non-overlapping elevational ranges in sympatry. d) The percentage of pairs that have gone through ES, ED, or niche conservatism (NC) to reach sympatric ranges with overlapping elevational distributions. Results are obtained from posterior-predictive simulations of the model-averaged parameter estimates.

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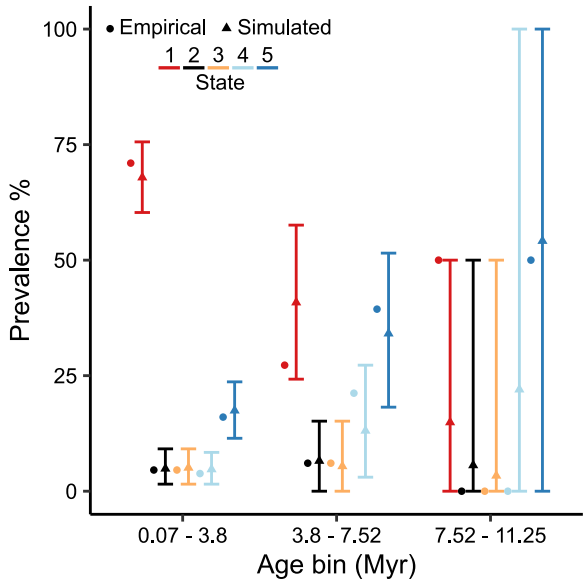

Figure 3 empirical prevalence and predicted prevalence of states by age category. Predicted prevalence (triangles) was obtained from posterior predictive simulations, and empirical data (circles) represents the prevalence of the states within three bins of equal age width starting at the youngest pair and ending at the oldest. Data among age groups is distributed unevenly (n = 131, 33, and 2). Brackets indicate the 95% confidence interval of the prevalence of the states across 1000 simulations.