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

Abstract

Aim

The coexistence and turnover of species along elevation gradients makes tropical mountains hotspots of biodiversity. However, understanding the historical processes through which species arising in geographic isolation (i.e. allopatry) assemble along the same mountain slope (i.e. sympatry) remains a major challenge. Multiple models have been proposed, (1) including the sorting of already elevationally divergent species, (2) the displacement of elevational niches upon secondary contact, potentially followed by convergence, or (3) niche conservatism, in which ancestral elevational niches are retained. However, the relative contribution of these processes to driving patterns of elevational overlap and turnover is unknown.

Location

Tropical mountains of Central- and South-America.

Time period

The last 12 myr.

Major taxa studied

Birds.

Methods

We collate a dataset of 166 avian sister pairs containing estimates of their phylogenetic age, geographical and regional elevational range overlap. We develop and apply a framework based on continuous-time Markov models to infer the relative frequency of different historical pathways in explaining the present day overlap and divergence of sympatric sister species along elevational gradients.

Results

We show that elevational sorting and displacement contribute almost equally to the turnover of closely related bird species across elevation gradients. In contrast, overlap of sister species along elevation gradients is almost entirely (>89%) explained by species attaining sympatry while elevational niches remain conserved.

Main conclusions

Bird communities across tropical elevation gradients are assembled through a mix of processes, including the sorting, displacement and conservatism of species elevation ranges. The dominant role of niche conservatism in explaining co-occurrence of species on mountain

slopes rejects more complex scenarios requiring niche displacement followed by subsequent expansion. The ability of closely related species to coexist without elevational divergence provides a more direct and thus faster route to sympatry and may help explain the exceptional species richness of tropical mountains.

Keywords: biotic interactions, character displacement, community assembly, elevational gradient, niche conservatism, species sorting, sympatry

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 (Weber *et al.*, 2017). These historical processes include speciation, niche evolution, dispersal, and range expansions (Mittelbach & Schemske, 2015), 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 (Pfennig & Pfennig, 2010; Stuart & Losos, 2013). 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 (Brown & Wilson, 1956). 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 (Cadena *et al.*, 2011) 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 (Pigot *et al.*, 2018).

A classic system for studying these historical processes concerns the distribution of vertebrates on tropical mountain slopes. Tropical mountains are renowned for their exceptional diversity. For instance, in the tropical Andes over 800 species of birds can be found living on a single mountain slope (Walker *et al.*, 2006). Since most speciation events involve the geographic isolation of populations on different mountains (i.e. allopatry)(Price, 2008; Cadena & Céspedes, 2020; Linck *et al.*, 2020), 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 hundred metres in vertical distance) and replace one another across the gradient (Diamond, 1973; Terborgh & Weske, 1975). Previous studies have variously provided evidence that conservatism in elevation niches, sorting, and displacement may individually be involved in shaping these patterns of range overlap 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 elevational niche conservatism (ENC) 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 (Cadena *et al.*, 2011) (Figure 1a). However, while some studies have argued that niche conservatism is a pervasive process (Linck *et al.*, 2021), the same pattern could also arise under the elevational displacement (ED) model. Under ED, 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 (Figure 1a). The ED model has also been proposed to be the dominant process explaining the build-up of species within elevation zones on tropical mountains (Diamond, 1973; Freeman, 2015).

A similar challenge exists when trying to discriminate elevational displacement from the elevational sorting (ES) model. Both these models predict that species living on the same mountain slope should have non-overlapping elevation ranges, at least prior to any subsequent expansion in elevation range. Thus, discriminating between these scenarios depends critically on inferences about whether elevational divergence precedes (i.e. ES) or is coincident with (i.e. ED) the attainment of secondary contact (Figure 1a). Studies attempting to address this issue have variously used phylogenetic information to infer the relative timing of elevational divergence and secondary sympatry or have compared elevation divergence between sister species in zones of sympatry to places where they remain allopatric (Freeman, 2015; Cadena & Céspedes, 2020). 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 and elevational turnover (Anderson & Weir, 2021). For example, there is no reason to think that only one of

these processes is determining the assembly of the remarkable bird diversity within the Andes. 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 elevational 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 sympatry using continuous-time Markov models (Pigot *et al.*, 2018), 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 (Phillimore *et al.*, 2008; Price, 2008), 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 patterns of geographic and elevational range overlap arise. Using this approach, we address three main objectives. First, what is relative importance of elevational sorting, displacement and niche conservatism in build-up of sympatry among Neotropical montane sister species? Second, what is the relative importance of elevational sorting and displacement in generating turnover between sister species across elevation gradients and how does co-occurrence (i.e. range overlap) 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

2.1 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 (Barker *et al.*, 2015; Harvey *et al.*, 2020). We only retained sister pairs that met the following conditions: (1) At least one of the species occupies montane habitat, defined as areas >500m above sea-level (Freeman, 2015). (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 test whether our conclusions were robust and to compare with previously published results that have using alternative statistical methods, we also reanalysed a previously published global dataset of montane sister species (Supplementary material, Figure S2)(Freeman, 2015).

We scored whether each sister pair was allopatric or sympatric and whether they had overlapping or non-overlapping elevational distribution using geographical and elevational range data gathered from a number of sources, including Stotz *et al.* (1996) and regional field guides and surveys (Hilty & Brown, 1986; Stotz *et al.*, 1996; Ridgely & Greenfield, 2001; Hilty, 2003; Walker *et al.*, 2006; Schulenberg *et al.*, 2007; Athanas & Greenfield, 2016; Vallely & Dyer, 2018). We supplemented this with *Birds of the World (BW)* (Billerman *et al.*, 2020) that typically reflects information found in local field guides but incorporates more recent taxonomic changes. We note that, although not primary scientific literature, field guides offer a wealth of expert knowledge on the natural history of birds and are frequently used in studies of bird elevation distributions, e.g. (Quintero & Jetz, 2018).

Our method requires treating geographical and elevational overlap as discrete states. We defined species as having overlapping elevation ranges if overlap was ≥20%. This threshold was chosen to avoid classing species which only meet marginally along narrow contact zones as overlapping. To test the robustness of our conclusions, however, we also repeated our analysis using different values (1, 10, and 30% overlap, Figure S1). Sympatry was defined as when sister species were present on the same mountain slope, regardless of whether this overlap was widespread (i.e. thousands of kms) or minimal (i.e. a few kms). We did not use metrics of absolute or proportional range overlap to define sympatry because this is unsuitable for montane systems where one species can have a very small geographic range. In practice, defining sympatry was unambiguous as allopatric pairs typically occurred on different mountain summits or regions 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 (Figure 1b). For sister species occurring in allopatry, they may have overlapping (state 1) or non-overlapping (state 3) elevational ranges. 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). We did not classify pairs in a separate state if they showed elevational divergence in allopatry but not sympatry (opposite of state 2). Such a state would be unimportant for interactions between sister species as elevational differentiation may not be required for sympatry, or be the cause of interactions with non-sister species.

We classified sister species to each state using the following protocol: (i) We determined if pairs were allopatric or sympatric and (ii) exhibited range-wide elevational overlap using Stotz *et al.* (1996) (and *BW* where taxonomy was outdated). (iii) Elevation ranges may vary regionally, and as a consequence species that have overlapping elevations at a range-wide scale may not overlap locally (Terborgh & Weske, 1975; Graves, 1988). For sympatric pairs that showed >10% range-wide elevational overlap we determined if species actually overlapped on a regional level using regional field guides covering each species' range. If (iiia) species showed <20% elevational overlap in all sympatric and allopatric regions, they were reassigned to state 4. Species were assigned to state 2 if (iiib) the sister species had overlapping elevation ranges in regions of allopatry but not sympatry (<20%) and (iiic) no other closely related species forms a hypothesised elevational replacement in the allopatric part of their range. This was to ensure that overlap in regions of allopatry was not caused by displacement from a tertiary species, as this would not be the result of interactions between the sister species. We assessed this using information on the geographic and elevational ranges of congeners as well as observations mentioned in field guides.

2.2 Statistical analysis using Markov models

To infer the relative importance of different assembly scenarios in explaining patterns of geographic and elevation overlap and turnover, we developed a continuous time multi-state Markov model (Figure 1b). 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 (Coyne & Orr, 2004). Sister pairs then stochastically transition between states, with different transition pathways corresponding to the different assembly scenarios. Under the ES model, 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 ED model, 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 ENC model is described by a direct transition from state 1 to sympatry and overlapping elevational ranges (state 5).

Once sympatry between sister species is attained (states 2, 4 or 5) elevational ranges may continue to change. Sister pairs in state 2 (i.e. elevation overlap in allopatry and non-overlap in sympatry), could 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 could 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)(Diamond, 1973). Our model thus allows for the elevation 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) (Jackson, 2011) 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) model combinations according to AIC and report both the best model and the model averaged parameter values of all highly supported models (ΔAIC $\leq$ 2 of best model).

2.3 Relative frequency of trajectories

Having inferred the transition rates between states, we then used these to estimate the relative contribution of elevational displacement (ED), elevational sorting (ES), and elevational niche conservatism (ENC) to pairs leaving state 1 and arriving in states 2, 4 and 5. Specifically, we used the inferred rates to perform 1000 posterior predictive simulations using the Gillespie algorithm for constant rates (Gillespie, 1977). 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 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 models (i.e. ED, ES, and ENC), and report the mean and standard deviation across simulations runs.

2.4 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.

2.5 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 model-averaged model fit to 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

3.1 Empirical distribution of sister pair states

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: 16%), with fewer pairs having non-overlapping elevational ranges and occurring in sympatry (state 4: 11%), or allopatry (state 3: 5%), or having non-overlapping elevational ranges in sympatry but overlapping elevational ranges in allopatry (state 2: 6%). 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: 3.35, state 3: 3.19, state 4: 3.88, and state 5: 3.41Myr), consistent with our assumption that is the initial state at the time of species divergence.

3.2 Transition rates between states

We found that our best model contains two parameters and constrains r12, r13, r15, r25, and r45 to 0.06 (CI95: 0.05-0.08), and r24, r34 to 0.44 (CI95: 0.25-0.75). While there are 27 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 the initial state of allopatry with overlapping elevation ranges (state 1) to non-overlapping elevation ranges, either while in allopatry (r13 = 0.06/Myr) or upon the attainment of sympatry (r12 = 0.06/Myr) is relatively slow, and similar to attaining sympatry while conserving elevational ranges (r15=0.07/Myr). Once elevational differentiation has occurred in either allopatry (state 3) or upon secondary contact (state 2), the transition to complete elevational differentiation (state 4) is relatively fast (r34=0.53/Myr and r24=0.32/Myr).

3.3 The relative contribution of community assembly routes

The posterior-predictive simulations show that following speciation a similar proportion of pairs embark on the ES (32.86%, CI95: 21.54-44.64%), ED (29.31%, CI95: 17.86-41.27%) and ENC routes (37.31%, CI95: 24.67-50.00%) (Figure 2b). Of the pairs with currently non-overlapping elevation ranges in sympatry (states 2 and 4), more are inferred to be generated through ED (61.99%, CI95: 41.93-79.31%) than ES (38.01%, CI95: 20.69-58.07%) (Figure 2c). However, confidence intervals on these estimates broadly overlap, suggesting there is little evidence that one route is more common than the other. Of the species pairs that attain overlapping elevation ranges in sympatry (state 5) almost all of these (89.29%, CI95: 75.84-100.0%) attain this state via the ENC route rather than the ES or ED pathways (Figure 2d). This can be explained because although a similar proportion of pairs embark on each pathway (i.e. r12 ≈ r13 ≈ r15), species pairs taking the ES (1->3->4->5) and ED (1->2->4->5 or 1->2-

>5) routes must pass through a number of intermediate states to attain overlapping elevation ranges in sympatry and this takes much longer than the direct ENC route (1->5). We note that relaxing our threshold at which we consider species to have overlapping elevation ranges resulted in qualitatively similar results (Figure S1).

3.4 Assessing model fit and the 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 simulation 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, the posterior-predictive simulations under the estimated parameter values shows that this does not affect the reliability of our conclusions regarding the relative contribution of different assembly models because we can 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 patterns of range overlap and turnover across tropical elevational gradients. However, because previous studies have focused on static biogeographic patterns and treated elevational sorting, displacement and niche conservatism as alternative explanations, their relative contribution 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 elevational sorting and displacement contribute almost equally to explaining the turnover of closely related bird species across elevation gradients. Finally, we show that the overlap of sister species along elevation gradients is almost entirely (>89%) explained by species attaining sympatry while elevational niches remain conserved, rejecting more complex scenarios requiring displacement followed by subsequent expansion in elevational ranges.

The high biodiversity of tropical mountains is associated with rapid turnover in community composition, as ecologically similar species replace one another up the mountain. Previous studies of montane birds have concluded that elevational displacement rather than sorting is the dominant process explaining such elevational replacements (Diamond, 1973; Freeman, 2015). 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 elevational 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 elevational sorting and displacement contribute approximately equally to explaining turnover among sister species across tropical elevation gradients.

While our analysis detects evidence of both elevational sorting and displacement, we find that sympatry is frequently reached without differentiation in elevation. We estimate ~44% of sister species living on the same mountain slope attain sympatry while conserving their ancestral elevation niche. 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 (Cadena *et al.*, 2011). 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 elevational 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 (6.45%) to current patterns of co-occurrence along elevation slopes.

Our finding that a high proportion of allopatric sister species directly transition to occupy overlapping elevations in sympatry need not suggest that competition or other negative species interactions are unimportant in limiting coexistence for these species. Indeed, evidence that interspecific competition limits elevational ranges is widespread in birds (Terborgh & Weske, 1975; Freeman & Montgomery, 2016; Freeman *et al.*, 2016, 2019). Instead, species attaining sympatry without diverging in their elevation range may 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 (Pigot *et al.*, 2018). Furthermore, the relative mix of different assembly processes may not be static over geological time. Given the relatively young age of many Neotropical montane radiations, and that there is little evidence for a slowdown in the rates of diversification (Weir, 2006; Harvey *et al.*, 2020), local niche space at any point along the elevational gradient may currently be far from saturated. As alternative niche dimensions become increasingly densely packed over time, it is possible that elevational sorting and displacement may become increasingly important routes to sympatry as has been suggested for New Guinean (Diamond, 1973) and Himalayan songbirds (Price *et al.*, 2014).

The relative mix of elevational sorting, displacement and niche conservatism inferred by our models pertains to Neotropical birds and the dynamics of community assembly may differ in 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 may underestimate the frequency of elevational displacement or sorting if this occurs among more distantly related species. Indeed, species that form elevational replacements along mountain slopes are often not sisters (Patton & Smith, 1992; García-Moreno & Fjeldså, 1999; Caro *et al.*, 2013). However, this is also unlikely to fully 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 (Weir & Price, 2011). 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 among sister species that have retained overlapping elevational ranges (14.21Myr), is substantially shorter than the lag time for species passing through the elevational sorting or displacement routes combined (18.06Myr). 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 without having to diverge into different elevational zones.

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 elevational sorting, elevational displacement, and elevational niche conservatism in shaping species distributions across montane gradients. A key next step will be to test how well our results generalise to different mountain regions or taxa that vary in their ecology. Such a comparative approach may be necessary to uncover why elevational 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 (MacArthur, 1958), perch height among Anolis lizards (Lister, 1976), or depth zonation in the Cichlid fish of East African rift lakes (Rodríguez & Lewis, 1997).

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Data Accessibility Statement

Data used in this study was compiled from previously published sources. Code and the data set are made publicly available on acceptance at .

Author contributions

Conceptualisation, XX1, XX3, XX4; data curation XX1, XX2; formal analysis, XX1; funding acquisition, XX4; investigation, XX1; visualisation, XX1; writing – original draft, XX1; writing – review and editing, XX1, XX2, XX3, XX4. All authors have read and agreed to submit the current version of the manuscript.

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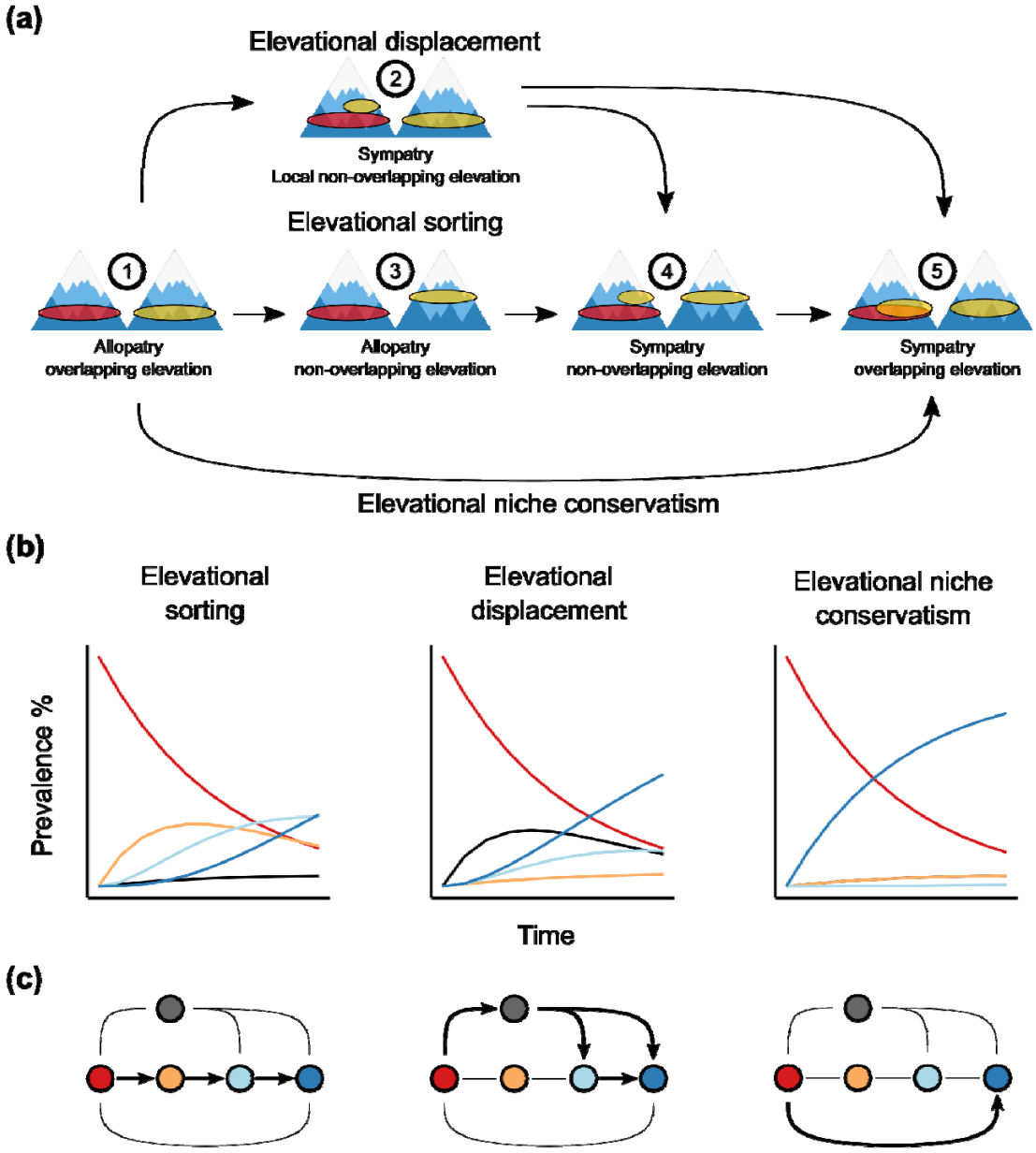

Figure 1 Hypothetical trajectories towards sympatry in montane sister species. a) All possible transitions in our models with their respective geographical and elevational context. (1) Species originate in allopatry and initially share the same elevational range. Subsequently, pairs might either stay 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) Elevational sorting (ES), II) Elevational displacement (ED) and

III) Elevational Niche conservatism (ENC). These hypotheses are based on simulations in which the respective pathways are dominant highlight the differences in temporal dynamics. c) An abstract view of the dominant transitions under respectively ES, ED, and ENC.

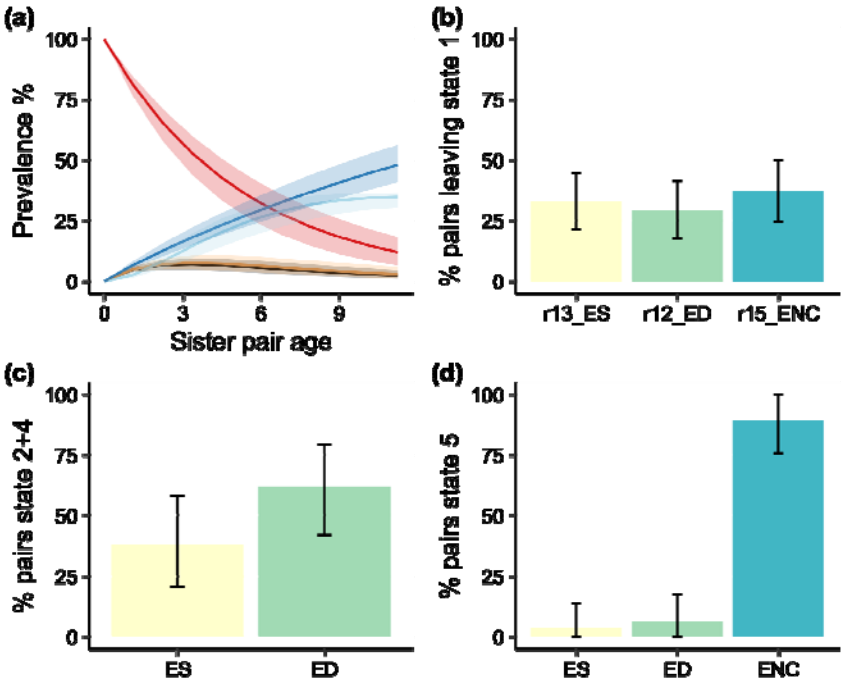

Figure 2 Sister species occurrence predictions through time and trajectories taken. a) predicted prevalence of the five states, as represented in Figure 1a, through time. State 2 and 3 overlap greatly in predicted prevalence. Shaded areas show 95% confidence intervals. b) Percentage of sister pairs that leave state 1 and start on each of the three routes towards sympatry. c) the percentage of pairs gone through either elevational sorting (ES) or elevational displacement (ED) that occupy non-overlapping elevational ranges in sympatry. d) The percentage of pairs that have gone through ES, ED, or elevational niche conservatism (ENC) to reach sympatric ranges with overlapping elevational distributions. Results are obtained from posterior-predictive simulations of the model-averaged parameter estimates (Results 3.2).

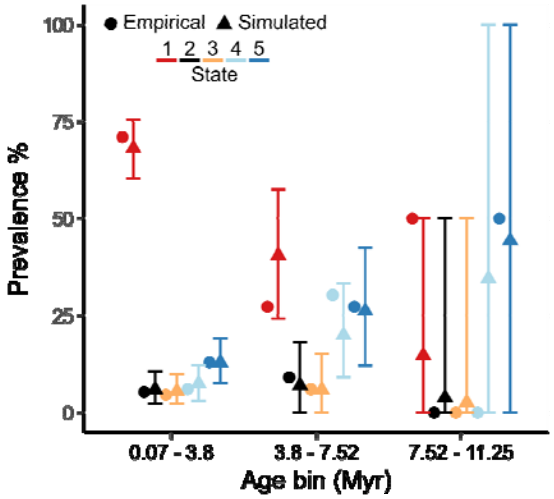

Figure 3 Empirical prevalence and predicted prevalence of states by age category. Predicted prevalence (triangles) was obtained from posterior predictive simulations, and empirical data (circles) represents the prevalence of the states within three bins of equal age width starting at the youngest pair 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.