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Competitive Interactions upon Secondary Contact Drive Elevational Divergence in Tropical Birds

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ABSTRACT: Tropical mountains harbor exceptionally high biodiversity, which is in part due to the marked elevational stratification of tropical biotas. However, the factors that influence the evolution of elevational distributions remain uncertain. I used a database of sister species of tropical montane birds from 41 families and three regions—the Neotropics, the Himalayas, and New Guinea—to test whether patterns of elevational divergence were consistent with (1) a stochastic process, (2) ecological sorting of elevational divergence that occurred in allopatry, or (3) elevational divergence driven by competitive interactions upon secondary contact. The stochastic and ecological sorting hypotheses predict that increased elevational divergence in sympatric sister species is explained by their greater evolutionary age, whereas the competitive interactions hypothesis predicts that elevational divergence is explained by geographical overlap. I found that genetic distances were unrelated to elevational divergence and that allopatric sister species occupied similar elevational distributions regardless of genetic distance in each region. Instead, sympatry was the only significant predictor of elevational divergence; regardless of evolutionary age, sympatric sister species had greater elevational divergence than allopatric sister species in each region, as predicted by the competitive interactions hypothesis. Importantly, this pattern occurred in all three geographic regions, which suggests that competition-driven elevational divergence upon secondary contact is a general process of community assembly in tropical montane avifaunas.

Keywords: community assembly, elevational gradient, interspecific competition, niche conservatism, niche evolution, tropical mountains.

Across taxa, biodiversity is concentrated in tropical latitudes (Mittelbach et al. 2007), with tropical mountains supporting disproportionately diverse biotas (Myers et al. 2000; Rahbek and Graves 2001; Jetz et al. 2004; Fjeldså et al. 2012). This montane megadiversity occurs at two well-characterized levels. First, species richness is high at any given location (α diversity), especially in lower-elevation

forests (Patterson et al. 1998). Second, most species are only found within narrow elevational zones, leading to high species turnover (β diversity) along elevational gradients (Patterson et al. 1998; Cadena et al. 2012). At an extreme, this turnover may involve closely related species that inhabit parapatric distributions along elevational gradients (elevational replacements; Diamond 1973; Terborgh and Weske 1975; Patterson et al. 1998; Freeman and Class Freeman 2014a).

That elevational specialization is rampant in tropical mountains is remarkable, because divergence in closely related species' climatic niche conditions is often minimal (Wiens et al. 2010; Cadena et al. 2012). This pattern—phylogenetic niche conservatism—can apply to climatic niches over both long (>5 million years; Peterson et al. 1999; Peterson 2011) and short (decades; Chen et al. 2011; Petitpierre et al. 2012) timescales and has been observed in phylogenetic analyses of extant taxa (e.g., Peterson et al. 1999; Peterson 2011), responses to recent climate change along elevational gradients (e.g., Chen et al. 2011; Freeman and Class Freeman 2014b), and during species introductions (e.g., Peterson 2011; Petitpierre et al. 2012). Given that phylogenetic niche conservatism appears to be pervasive, how do closely related tropical taxa diverge to inhabit different elevational zones?

This question can be explored by identifying the non-mutually exclusive ecological and evolutionary forces that could override niche conservatism and drive elevational divergence. Because speciation is typically allopatric (e.g., for birds; Barraclough and Vogler 2000; Price 2008), instances of elevational divergence between related species found along the same mountain slope result from successful range expansions that bring species into secondary contact following allopatric speciation. There are three processes that could generate such elevational divergence. First, elevational divergence may simply be a stochastic process correlated with the amount of time that has passed since species last shared a common ancestor. Elevational

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divergence among closely related taxa may be opposed by stabilizing selection, gene flow, and the genetic constraint of shared evolutionary history, with the probability of divergence increasing with greater evolutionary time (reviewed in Wiens et al. 2010). This stochastic model of elevational divergence therefore predicts that more closely related species should have more similar elevational distributions than distantly related species. Additionally, this model predicts that variance in elevational divergence should increase with genetic distance when comparing closely related species, such that few species should have low genetic distances and high elevational divergence (i.e., a scatterplot of genetic distance vs. elevational divergence would exhibit a triangular distribution). Because range expansions following allopatric speciation are necessary to lead to sympatry (defined here as two species found along the same mountain slope), sympatric species tend to be older than allopatric species (Weir and Price 2011; Pigot and Tobias 2013; Price et al. 2014; Tobias et al. 2014). Thus, a purely stochastic model predicts that, due to the greater average evolutionary age of sympatric species, elevational distributions should be more divergent in sympatric species than allopatric species (Tobias et al. 2014; fig. 1).

Second, ecological interactions during secondary contact may act as a sorting mechanism, permitting species that have evolved sufficiently divergent elevational distributions in allopatry to successfully attain sympatry following secondary contact (Cadena 2007). The ecological sorting hypothesis parallels the stochastic hypothesis in assuming elevational divergence generally increases with evolutionary time, but it differs in positing that a deterministic mech-

anism influences the likelihood that sister species become sympatric upon secondary contact. Specifically, the sorting model assumes that competition based on limiting similarity prevents sympatry between sister species with similar elevational distributions when range expansions bring them into secondary contact but allows sympatry between sister species if their elevational distributions have diverged sufficiently while in allopatry (Cadena 2007; Pigot and Tobias 2013). Because the elevational divergence that allows sister species to become sympatric in the sorting hypothesis becomes more likely to evolve with increasing evolutionary time, the sorting hypothesis also predicts that greater elevational divergence in sympatric species is primarily explained by their greater evolutionary age (fig. 1).

Third, competitive interactions upon secondary contact may drive elevational divergence between closely related species (Diamond 1973). Although the ecological sorting hypothesis proposes that competition in secondary contact sorts preexisting divergence, the competitive interactions hypothesis proposes that competitive interactions in secondary contact actively drive divergence. For example, the negative impact of strong interference interspecific competition between sister taxa in secondary contact could drive spatial segregation to reduce interspecific interactions (Diamond 1973). Equally, apparent competition mediated by species-specific predators or pathogens could cause closely related, ecologically similar species to partition elevational space upon secondary contact (Ricklefs 2010). Similar to the first two hypotheses, the competition hypothesis predicts that elevational distributions should be more divergent in sympatric species than in allopatric

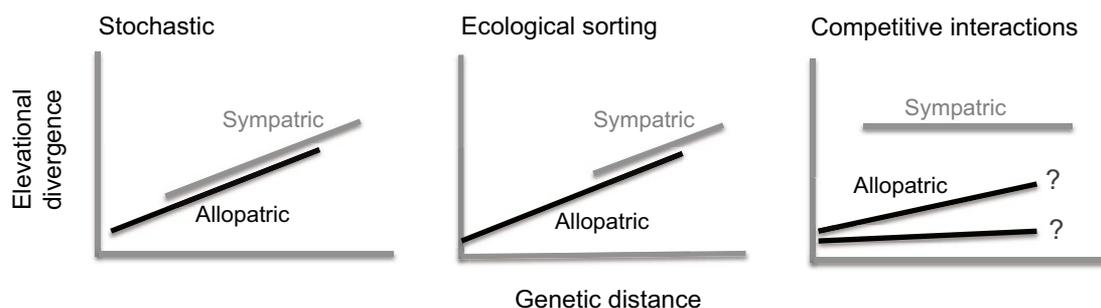


Figure 1: Three evolutionary processes to explain elevational divergence predict different relationships for how elevational divergence evolves over time in sympatric and allopatric sister species. All three processes assume that speciation is allopatric. Importantly, all three hypotheses predict that sympatric sister species have greater elevational divergence than allopatric sister species. The stochastic and sorting hypotheses predict that this difference is attributable to the older age of sympatric sister species and that rates of elevational divergence are similar in allopatry and sympatry. The sorting hypothesis additionally predicts that only sister species with relatively high elevational divergence will successfully attain sympatry, whereas those with relatively low elevational divergence will remain allopatric. In contrast to the stochastic and sorting hypotheses, the competitive interactions hypothesis predicts that elevational divergence is explained by geographical overlap, with sympatric sister species tending to have higher elevational divergence than allopatric sister species regardless of genetic distance. In the competitive interactions hypothesis, elevational divergence in allopatry may either increase with genetic distance or remain low, depending on the strength of phylogenetic niche conservatism.

species. However, it differs by predicting that geographic overlap (i.e., sympatry vs. allopatry) and not evolutionary age explains elevational divergence (fig. 1).

I tested the predictions of these hypotheses using data on sister species of birds found in the humid tropical mountains of three regions that are largely biogeographically independent—the Neotropics, the Himalayas, and New Guinea. Although elevational specialization is observed in many tropical taxa (e.g., mammals: Patterson et al. 1998; butterflies: Hall 2005), birds are the only large group with both published, high-quality, range-wide elevational distribution data and many species-level phylogenies available for multiple geographic montane regions. They therefore provide a suitable taxonomic focus for investigating this question. Explaining tropical montane megadiversity requires understanding elevational specialization; although previous research has investigated this question for specific case examples, I conducted the first broad comparative analysis to test the evolutionary mechanisms that drive elevational divergence in tropical birds in multiple independent geographic regions.

Methods

I used a sister species approach to evaluate hypotheses explaining elevational divergence in tropical montane avifaunas of three regions: the Neotropics, the Himalayas, and New Guinea. The evolution of elevational distributions could be profitably explored with other phylogenetic approaches, such as using closely related groups of species as the unit of analysis (e.g., Weir and Price 2011). Because most elevational replacements are not sister taxa (Patton and Smith 1992; Cadena 2007), such an approach could potentially bias results toward the competitive interactions hypothesis. I used sister species as my unit of analysis to avoid such problems and also to make unbiased comparisons of genetic distances between allopatric and sympatric sister species.

I identified sister species by performing a thorough survey of published molecular phylogenies of landbirds resident in the Neotropics, the Himalayas, and New Guinea, three tropical montane regions with diverse avifaunas. Most phylogenies were inferred from a combination of mitochondrial and nuclear markers, although a small number of older studies that used mitochondrial data alone were included. When multiple phylogenies were available for the same clade, I used the most recent study to infer sister species relationships.

To minimize erroneous classification of sister species, I considered only molecular phylogenies that sampled >80% of species within a genus. A small number of well-sampled phylogenies identified members of different genera as sister species ($n = 15$). Given the relative lack of published phylo-

genetic information for New Guinean birds, I additionally included species from New Guinea genera that contain only two species ($n = 13$) as sister species. The aim of this study was to investigate elevational divergence in species inhabiting humid tropical mountains where climatic differences between regions are relatively small (as opposed to arid mountains; McCain 2009). I therefore used regional reference volumes (e.g., Beehler et al. 1986; Stotz et al. 1996; Robson 2008) to restrict my analysis to sister species where both taxa inhabit primarily humid climates. Although the majority of sister species pairs in my database were restricted to montane distributions, I also included species pairs where one species is montane and the other is found primarily in lowland environments.

Elevational Divergence

I calculated elevational divergence between sister species pairs on the basis of the species with the narrower elevational distribution. Elevational divergence was the proportion of this species' elevational distribution that overlapped with the elevational distribution of its sister species. This metric ranged from zero, where the elevational distribution of the species with the smaller elevational range was entirely subsumed within the broader elevational range of its sister species, to one, where sister species occupied non-overlapping elevational distributions. Species with wide distributions in humid Neotropical mountains typically occupy consistent elevational zones across the latitudinal gradient (Graves 1988; Stotz et al. 1996). Therefore, I assigned elevational distributions at the range-wide level for all species, using single sources for each region (New Guinea: Beehler et al. 1986; Himalayas: Del Hoyo et al. 1992; Neotropics: Stotz et al. 1996). For a small number of species described after the publication of these single sources (e.g., Coopmans and Krabbe 2000), I garnered elevational distribution data from field guides (e.g., Ridgely and Greenfield 2001).

Measuring elevational distributions at the range-wide level does not account for sister species that occupy divergent elevational distributions where they are sympatric but expanded distributions where they are allopatric (e.g., Diamond 1973; Remsen and Graves 1995; there are ~13 examples in my database). These case studies constitute the best distributional evidence that competitive interactions in secondary contact may drive elevational divergence (Diamond 1973, 1986). However, my approach classifies such cases as sympatric sister species with low elevational divergence, biasing my analysis against the competitive interactions hypothesis. It would be optimal to compare elevational distributions of sympatric species in both the sympatric and allopatric portions of their distributions when applicable. However, doing so would require eleva-

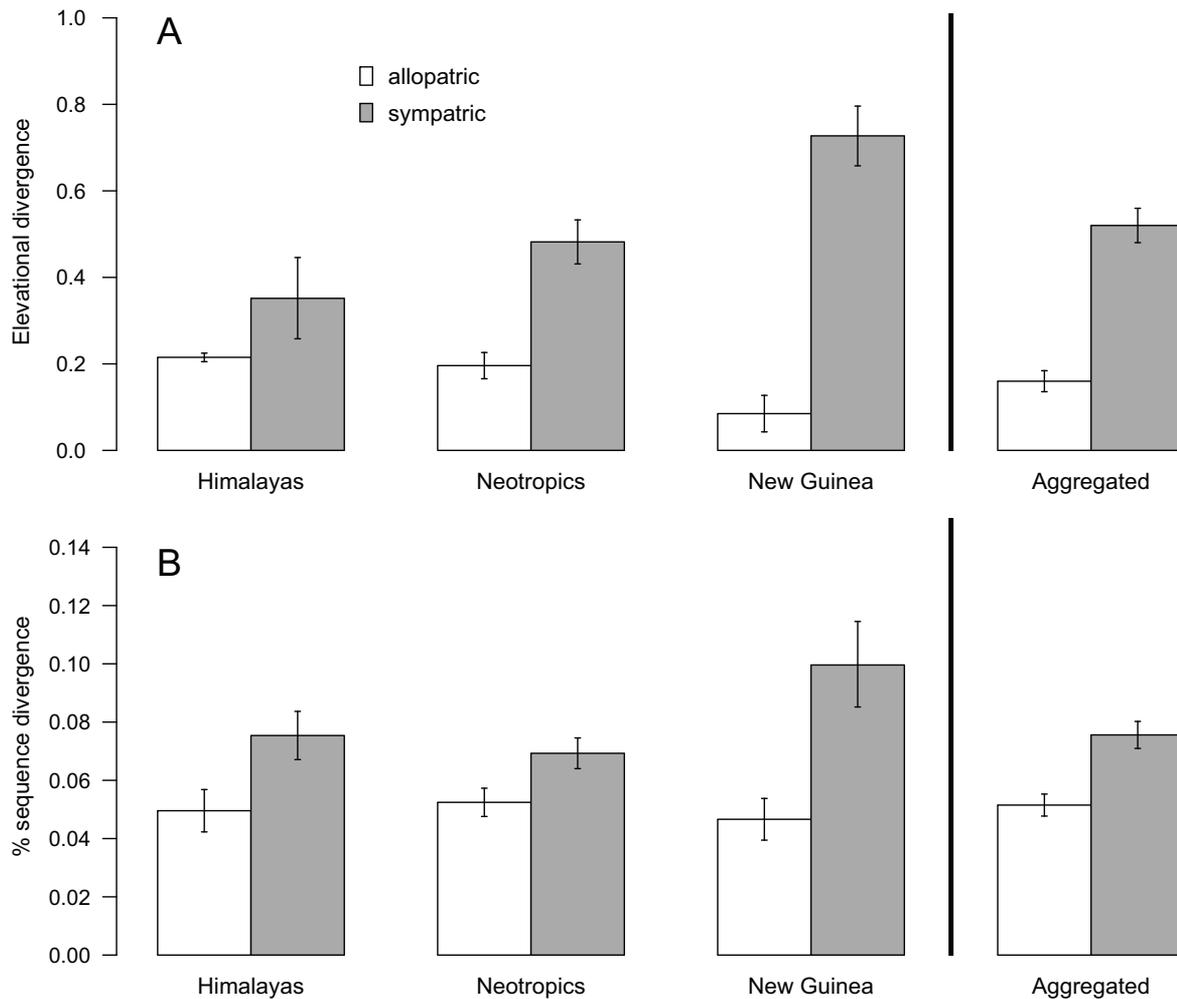


Figure 2: Elevational divergence (A) and genetic distance (B) are both greater in sympatric avian sister species than in allopatric avian sister species in each montane region. Bars illustrate mean values \pm standard errors. Elevational divergence is based on range-wide elevational distributions (Neotropics: $n = 136$; Himalayas: $n = 35$; New Guinea: $n = 32$), and genetic distance is measured as percentage sequence divergence in mitochondrial DNA (Neotropics: $n = 125$; Himalayas: $n = 34$; New Guinea: $n = 23$). In all three regions, sympatric sister species have significantly higher elevational divergence and larger genetic distances than allopatric sister species.

tional distribution information gathered at a local scale (e.g., a single mountain or mountain range) that simply does not exist for many regions. I therefore followed the conservative course of using single reference volumes to measure elevational distributions at the range-wide level.

Geographical Overlap

I used digital distribution maps (Ridgely et al. 2003) and regional field guides (Beehler et al. 1986; Del Hoyo et al. 1992; Ridgely and Tudor 2009) to assign sister species to two categories of geographical overlap: allopatric or sympatric. Allopatric sister species inhabited completely non-overlapping geographic distributions. Typically, allopatric

sister species in my database inhabited distinct montane regions separated by lowland barriers. In contrast, I classified sister species that were present on the same mountain slope as sympatric. This designation therefore included sister species with both widespread and minimal (i.e., parapatric) elevational overlap. Although analyses that considered geographic range overlap as a quantitative trait could also be used to investigate elevational divergence, pervasive asymmetries in range sizes would likely obscure any possible relationship between geographical overlap and elevational divergence (e.g., even species with nearly identical elevational distributions in sympatry often differ markedly in their overall range size and would thus be categorized as having low range overlap). Moreover, the

key question addressed in this study is whether sister species that likely interact ecologically over relatively short time scales (i.e., are present on the same mountain slope; Price et al. 2014) differ in elevational divergence from geographically isolated (allopatric) sister species that do not interact ecologically. Thus, I used allopatric and sympatric as the sole categories of geographical overlap for analyses.

Genetic Distances

I obtained homologous mitochondrial DNA sequences from GenBank for most sister species. I then calculated uncorrected sequence divergence (p distances) between sister species in MEGA5 (Tamura et al. 2011). Mitochondrial DNA sequences have been considered to represent neutral loci that evolve in a relatively clocklike fashion (Weir and Schluter 2008). If so, these measures of sequence divergence serve as a proxy for time since the sister species last shared a common ancestor. Recent evidence that suggests mitochondrial DNA sequences may not necessarily be neutral loci (Dowling et al. 2008; Ribeiro et al. 2011) calls into question the assumption that mitochondrial divergence is an accurate proxy for time. Nevertheless, because there is no a priori expectation that rates of mitochondrial divergence differ between allopatric and sympatric sister species of tropical montane birds, my analysis should be robust to the assumption that mito-

chondrial DNA sequences are selectively neutral. However, limited introgression upon secondary contact could lead to a systematic reduction in the genetic distances of sympatric sister species relative to allopatric sister species. The majority of sympatric sister species in my database have relatively large divergences in mitochondrial DNA (e.g., <10% of the sympatric sister species in my analysis have genetic distances <3%), and these closely related sympatric sister species tend to have low degrees of elevational divergence. Although introgression may have occurred in some cases included in my analysis, dealing with introgression is beyond the scope of this article, and there is no clear post hoc method to identify which sister species in my database may have hybridized upon secondary contact.

Statistical Analysis

I used linear regression models and corrected Akaike information criterion (AICc)-based model selection to test hypotheses to explain elevational divergence in sister species pairs. I developed a complete set of models to predict elevational divergence, with genetic distance, geographical overlap (sympatry or allopatry), and region (the Neotropics, the Himalayas, and New Guinea) as predictor variables. I considered all interaction terms between these predictor variables and used AICc scores to select the best-supported model, using the MuMIn package in R to perform model

Table 1: Models to predict elevational divergence in tropical montane birds

Parameters in model	df	AICc	Δ AIC	Model weight
Genetic distance + geographical overlap + genetic distance \times region	6	103.8	0	.39
Genetic distance + geographical overlap + geographical overlap \times region	8	105	1.27	.20
Genetic distance + geographical overlap + genetic distance \times geographical overlap + genetic distance \times region	7	105.8	2.04	.14
Genetic distance + geographical overlap + genetic distance \times geographical overlap + genetic distance \times region + geographical overlap \times region + genetic distance \times geographical overlap \times region	11	106.7	2.91	.09
Genetic distance + geographical overlap + genetic distance \times geographical overlap + geographical overlap \times region	9	107.2	3.47	.07
Genetic distance + geographical overlap + genetic distance \times region + geographical overlap \times region	8	107.3	3.58	.06
Genetic distance + geographical overlap + genetic distance \times geographical overlap + genetic distance \times region + geographical overlap \times region	9	109.5	5.74	.02
Geographical overlap + geographical overlap \times region	7	109.9	6.1	.02
Genetic distance + geographical overlap	4	111.6	7.84	.01
Genetic distance + geographical overlap + genetic distance \times geographical overlap	5	113.5	9.75	0
Geographical overlap	3	122.7	18.95	0
Genetic distance + genetic distance \times region	5	139.7	35.97	0
Genetic distance	3	147.6	43.84	0

Note: AIC = Akaike information criteria; AICc = corrected Akaike information criteria; df = degrees of freedom.

selection and model averaging (R Development Core Team 2014).

Results

The final database is deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.6qg3g> (Freeman 2015). It includes information on 203 sister species pairs from 41 families (136 in the Neotropics, 35 in the Himalayas, and 32 in New Guinea). I obtained sequence data for 182 of these sister species pairs: 125 from the Neotropics, 34 from the Himalayas, and 23 from New Guinea. Sympatric sister species ($n = 96$) had significantly greater elevational divergence than allopatric sister species ($n = 107$; 0.52 ± 0.39 vs. 0.16 ± 0.25 ; Wilcoxon rank sum test: $W = 2,493$, $P < .0001$; fig. 2; summary statistics presented are mean value \pm SD). In addition, as expected given the dominance of allopatric speciation in birds (Price 2008), allopatric sister species ($n = 99$ with sequence data) had smaller genetic distances than sympatric sister species ($n = 83$ with sequence data; $0.052 \pm .034$ vs. 0.076 ± 0.041 ; Wilcoxon rank sum test: $W = 2,785$, $P = .0001$; fig. 2). These patterns—that sympatric sister species are both older and more divergent in elevational distribution than allopatric sister species—are compatible with all three hypotheses. Thus, I used model results to test the different patterns of elevational divergence over time in allopatry and sympatry predicted by the different hypotheses (Martin et al. 2010; Pigot and Tobias 2013; Tobias et al. 2014; see fig. 1).

The best model to predict elevational divergence contained three parameters (genetic distance, geographical overlap, and a genetic distance \times region interaction term; see table 1). Because the second and third best-supported models had comparable AICc scores and relatively high model weights (table 1), I used model averaging to combine the top three models into the final model (table 2). This final

averaged model thus contained a geographical overlap \times region interaction term as an additional parameter (table 2). Although the final averaged model contained the four parameters described above, the only significant predictor of elevational divergence was geographical overlap; sympatric sister species had significantly greater elevational divergence than allopatric sister species (table 2; fig. 3). In contrast, there was no effect of genetic distance on elevational divergence in the final averaged model (table 2; fig. 3). Importantly, these key results were robust to different approaches to model selection; whether I considered the top three models in isolation, the top two models combined in an average model, or the top three models combined in an averaged model as presented in table 2, sympatry was the only significant predictor variable (P values were always $<.001$), and the genetic distance parameter was never significant (P values ranged from .18 to .71). Although regions varied in the effect of genetic distance and geographical overlap on elevational divergence (table 2; figs. 2, 3), the pattern of increased elevational divergence in sympatric sister species compared with allopatric sister species, regardless of genetic distance, was consistent across regions (fig. 3).

Discussion

My results support the hypothesis that competitive interactions upon secondary contact drive elevational divergence in tropical montane avifaunas. I found that elevational divergence between sister species of tropical montane birds in the Neotropics, the Himalayas, and New Guinea is predicted by geographical overlap and not by genetic distance; sympatric sister species had greater elevational divergence than allopatric sister species regardless of genetic distance (fig. 3; table 2). This result demonstrates that sympatry is often required to generate elevational divergence

Table 2: Final averaged model to predict elevational divergence between sister species of tropical montane birds

Parameter	Estimate	Standard error	Approximate 95% confidence interval	Z	P
(Intercept)	.11	.087	-.06 to .28	1.25	.21
Genetic distance	-.83	1.16	-3.15 to 1.49	.71	.48
Geographical overlap (sympatric)	.33	.081	.17-.49	4.01	<.0001
Genetic distance \times region (New Guinea)	2.59	1.84	-1.09 to 6.27	1.41	.16
Genetic distance \times region (Neotropics)	1.04	.98	-.92 to 3.05	1.06	.29
Geographical overlap (allopatric) \times region (Neotropics)	.047	.088	-.13 to .22	.53	.60
Geographical overlap (sympatric) \times region (Neotropics)	.036	.074	-.11 to .18	.49	.63
Geographical overlap (allopatric) \times region (New Guinea)	.018	.077	-.14 to .17	.23	.82
Geographical overlap (sympatric) \times region (New Guinea)	.010	.17	-.33 to .35	.59	.56
Genetic distance \times geographical overlap (sympatric)	-.009	.62	-1.25 to 1.23	.15	.89

Note: Approximate confidence intervals were calculated as the parameter estimate $\pm 2 \times$ standard error. P values for parameter significance were calculated by MuMIn in R (R Development Core Team 2014) after model averaging.

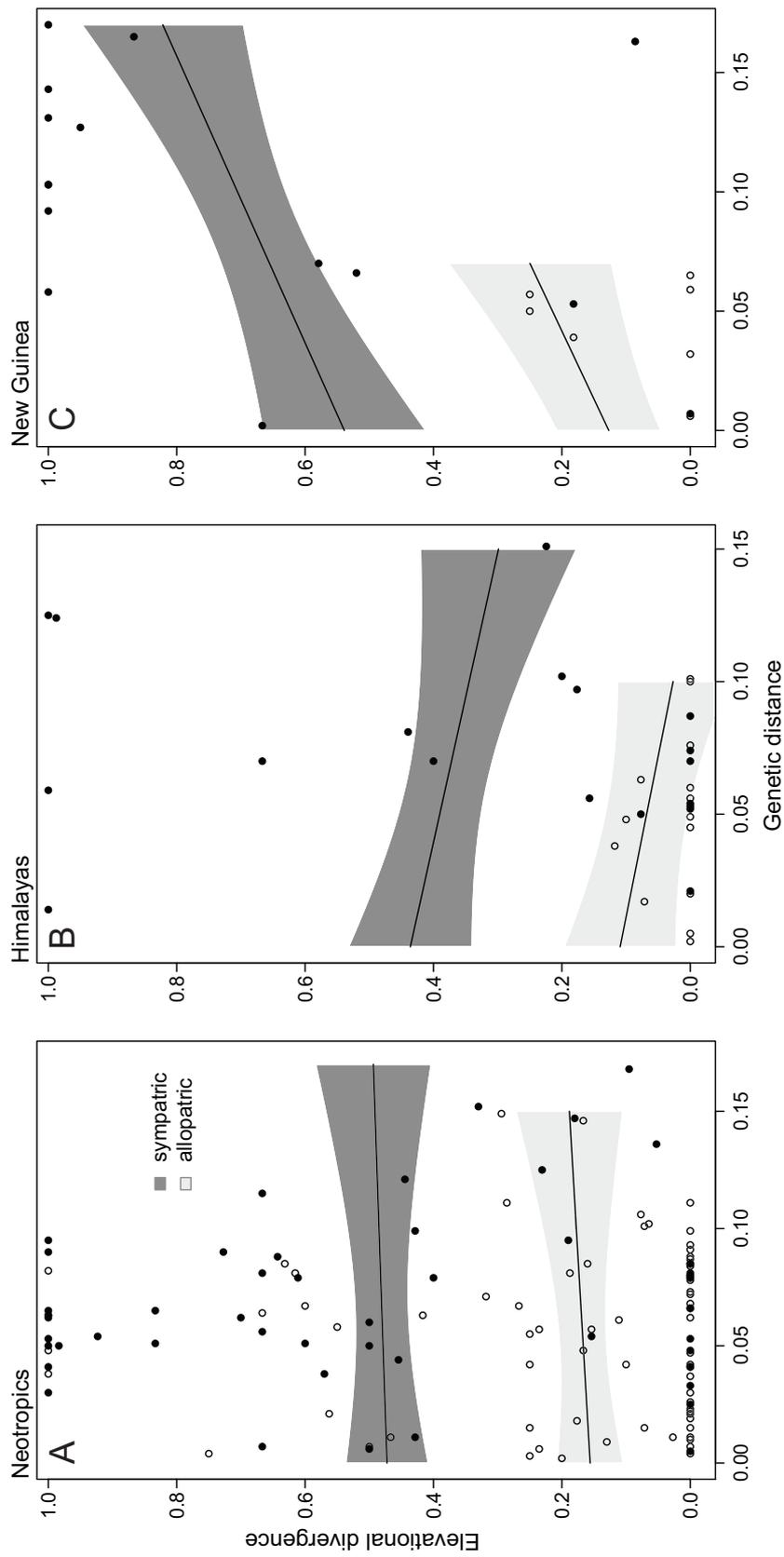


Figure 3: Model predictions show greater elevational divergence in sympatric sister species than in allopatric sister species of tropical montane birds over a range of genetic distances in the Neotropics (A), the Himalayas (B), and New Guinea (C). Trendlines show predictions of the final averaged model presented in table 2, with standard error shaded. Raw data are plotted as filled (sympatric sister species pairs) or open (allopatric sister species pairs) circles. Because the final averaged model did not include a region \times geographical overlap parameter, the slopes for sympatric and allopatric sister species within a single region are parallel. Model predictions are illustrated over the range of genetic distances present in the data for each region and category of geographical overlap.

between sister species, consistent with predictions of the competitive interactions hypothesis.

In contrast, this result is not consistent with the stochastic and ecological sorting hypotheses, which both predict that elevational divergence is largely a function of evolutionary age. The stochastic and ecological sorting hypotheses also predict that examples of sister species with high elevational divergence but low genetic distances should be rare, yet there are many such examples in my data set. In addition, the ecological sorting hypothesis assumes that the niche differences that eventually permit sympatry evolve in allopatry. However, elevational distributions in allopatric sister species diverged minimally even at large genetic distances (fig. 3). Hence, elevational distributions that evolved in allopatry do not appear to provide much variation that could be sorted upon for tropical montane birds, at least when considering the database of sister species that I used. Thus, the geographically replicated patterns that I found are most consistent with the hypothesis that competitive interactions upon secondary contact drive divergence in elevational distributions between sister species of tropical montane birds.

However, it is important to recognize that ecological sorting could generate the observed patterns if range expansions are assumed to be highly probable at all times. In this scenario, range expansions are sufficiently frequent that sister species that evolve divergent elevational distributions in allopatry soon undertake range expansions that lead to successful sympatry, explaining why sister species with divergent elevational distributions tend to be sympatric regardless of evolutionary age. The flip side to this scenario is that range expansions that brought sister species inhabiting similar elevational distributions into secondary contact would be both frequent and unsuccessful, and such sister species would remain allopatrically distributed. Although the ecological sorting hypothesis likely applies to specific case examples of tropical montane birds (e.g., Cadena 2007), the assumption that range expansions that lead to secondary contact are equally high for all species is unlikely to be true for tropical birds. Instead, geographic and behavioral barriers to dispersal likely limit the probability of range expansions in tropical birds (Price 2008; Burney and Brumfield 2009; Weir and Price 2011; Salisbury et al. 2012; Smith et al. 2014).

My results demonstrate that elevational divergence in tropical montane birds is driven by a factor that affects sympatric sister species but not allopatric sister species. Competitive interactions that occur during secondary contact, such as interference interspecific competition (Diamond 1973) and apparent competition driven by species-specific predators and parasites (Holt and Lawton 1994; Ricklefs 2010), are likely processes that could drive elevational divergence between sister species of tropical montane birds. Resource competition between avian sister spe-

cies upon secondary contact is expected to be intense due to high dietary niche overlap (Price 2008). Case studies of natural experiments, where species inhabit broader elevational distributions in the absence of a congener, are consistent with the hypothesis that interspecific competition influences elevational distributions of tropical montane birds (Diamond 1973, 1986; Terborgh and Weske 1975; Cadena and Loiselle 2007). In contrast, the possibility that species-specific enemies (predators and parasites) drive elevational divergence has not been rigorously tested, although a recent review of the causes of species' warm-edge limits did not find any case examples where these range limits were set by pathogens (Cahill et al. 2014). Additional research testing the processes that drive elevational divergence in particular case studies of sympatric tropical montane birds (or other taxa) are necessary to fully evaluate mechanisms underlying the competitive interactions hypothesis.

The interpretation that competition drives elevational divergence rests on the assumption that allopatric speciation, not parapatric speciation (e.g., Patton and Smith 1992; Smith et al. 1997), is the dominant geographic mode of speciation in tropical montane birds. Applied to elevational gradients, parapatric speciation models propose that an ancestral species with a broad elevational distribution speciates in situ into low- and high-elevation species that are sister species inhabiting divergent elevational distributions. Parapatric speciation could thus explain why sympatric sister species inhabit divergent elevational distributions regardless of elevational age. However, molecular studies of species thought to be likely candidates for parapatric speciation typically reveal that reproductive isolation evolved in allopatry (e.g., Cadena 2007; Fuchs et al. 2011). Given that the primacy of allopatric speciation in birds is well established (Barraclough and Vogler 2000; Price 2008; Pigot and Tobias 2013; Price et al. 2014), it seems unlikely that parapatric speciation is sufficiently common to be an important driver of observed patterns of elevational divergence in my database.

In conclusion, my results support the hypothesis that competitive interactions upon secondary contact are a common mechanism driving elevational divergence in tropical montane birds. Although varying scenarios may explain elevational divergence in specific case examples, I found broad support for the competitive interactions hypothesis in a diverse range of taxa in each of three geographically and phylogenetically independent avifaunas, suggesting the competitive interactions hypothesis may apply broadly to community assembly in tropical montane avifaunas. By driving the niche divergence that allows related species to occur sympatrically, competitive interactions may play a creative role in the assembly of diverse communities along elevational gradients (Schluter 2000). Future tests with additional taxonomic groups across a range of latitudes can test the generality of this model of community assembly.

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The blue jewel-babbler (*Ptilorrhoa caerulescens*, left) lives in the lowland forests of New Guinea, while its sister species, the chestnut-backed jewel-babbler (*Ptilorrhoa castanonota*, right), is found at higher elevations in the foothills. Photo credit: Benjamin G. Freeman.