ECOGRAPHY

Research

Behavior influences range limits and patterns of coexistence across an elevational gradient in tropical birds

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Does competition influence patterns of coexistence between closely related taxa? Here we address this question by analyzing patterns of range overlap between related species of birds ('sister pairs') co-occurring on a tropical elevational gradient. We explicitly contrast the behavioral dimension of interspecific competition (interference competition) with similarity in resource acquisition traits (exploitative competition). Specifically, we ask whether elevational range overlap in 118 sister pairs that live along the Manu Transect in southeastern Peru is predicted by proxies for competition (intraspecific territorial behavior) or niche divergence (beak divergence and divergence times, an estimate of evolutionary age). We find that close relatives that defend year-round territories tend to live in non-overlapping elevational distributions, while close relatives that do not defend territories tend to broadly overlap in elevational distribution. In contrast, neither beak divergence nor evolutionary age was associated with patterns of range limitation. We interpret these findings as evidence that behavioral interactions – particularly direct territorial aggression – can be important in setting elevational range limits and preventing coexistence of closely related species, though this depends upon the extent to which intraspecific territorial behavior can be extended to territorial interactions between species. Our results suggest that interference competition can be an important driver of species range limits in diverse assemblages, and thus highlight the importance of considering behavioral dimensions of the niche in macroecological studies.

Keywords: competition, elevational gradient, exploitative competition, interference competition, limiting similarity, range limits

Introduction

Understanding the factors that limit species' distributions is a longstanding goal of ecology (Wallace 1876). One profitable approach to studying range limits is to consider the distributions of closely related species that occur within the same region (Connell 1961, Whittaker 1967, Diamond 1973). For example, many previous studies have focused on how competition for shared limiting resources (exploitative competition) can shape the ranges of related taxa, based on the assumption that species efficient

at acquiring resources may be able to exclude less efficient competitors (Gause 1934, Hardin 1960, Tilman 1977). An alternative perspective is that behavioral interactions (interference competition) among related species may limit coexistence and thus determine range limits (Grether et al. 2017). However, few studies have explicitly considered the behavioral dimension of interspecific competition, and whether it contributes to patterns of geographical range limitation (Pasch et al. 2013).

Elevational gradients provide an excellent system to address the degree to which competition limits species' ranges. Mountain slopes encompass large environmental variation over a short geographic scale, maximizing the number of closely related species that occur within the same region while minimizing the influence of dispersal constraints on explaining why species live where they do. Interspecific competition is a historically popular hypothesis to explain why species live within only small sections of large elevational gradients (Brown 1971, Diamond 1973, Terborgh and Weske 1975). Although the precise mechanism of interspecific competition is seldom investigated, recent behavioral studies have uncovered cases where range limits along mountain slopes are set in part because species defend territories against related and ecologically similar taxa (Jankowski et al. 2010, Freeman et al. 2016). For example, two species of singing mice (*Scotinomys* spp.) live in distinct elevational zones in Central America; behavioral trials and removal experiments show that the behaviorally dominant higher elevation species exhibits territorial aggression that prevents the lower elevation species from expanding upslope (Pasch et al. 2013). These examples provide some support for a possible key role of behavior in limiting coexistence between close relatives – consistent with MacArthur's (1972) claim that 'behavior reduces a chaotic scramble to an orderly contest'.

These previous findings raise two key questions. First, is the effect of competition restricted to scattered case studies, or does it provide a more general explanation of species' elevational range limits in diverse assemblages? Second, is the mechanism by which competition sets elevational range limits linked to exploitative competition, or interference competition? These categories of competition are interrelated because aggressive behavioral interactions likely arise as an adaptive response to underlying competition for resources – i.e. interference competition is based on exploitative competition (Schoener 1983).

To address these two questions, we investigated the distributions of closely related species pairs in a diverse avifauna distributed along a well-studied Andes-to-Amazon elevational gradient with high quality distributional data (Patterson et al. 1998, Walker et al. 2006, Merkord 2010, Dehling et al. 2014, Trisos et al. 2014, Albrecht et al. 2018). Specifically, we used trait-based and phylogenetic models to investigate the relative importance of resource acquisition traits versus behavioral traits in determining patterns of range overlap within pairs of closely related species. Speciation in vertebrates is typically initiated in geographic

isolation (e.g. for birds; Price 2008), and cases where related species live today along the same elevational gradient are the result of range expansions and secondary contact (Patton and Smith 1992). Further, competition upon secondary contact in tropical montane birds, including in the Andes, is associated with elevational divergence and reduced overlap in elevational ranges (Freeman 2015). Here, we investigate how traits associated with exploitative and interference competition are related to observed patterns of elevational range overlap between pairs of closely related species (see also Fig. 1). For exploitative competition, we measured 1) niche divergence in a resource acquisition trait (beak morphology), because species with similar beaks are predicted to compete for resources more so than species with divergent beaks (Grant and Grant 2006, Pfennig and Pfennig 2012, Pigot et al. 2018), and 2) evolutionary age, measured as divergence times (time since species last shared a common ancestor), because closely related species are thought to generally experience greater competition than distantly related species (Cavender-Bares et al. 2009, Pfennig and Pfennig 2012, Price et al. 2014). For interference competition, we measured strength of intraspecific territorial behavior, which indicates both overall aggression linked to resource defense and the potential for interspecific territoriality (Ulrich et al. 2018). In sum, our comparative study offers one of the first tests of the relative importance of two interrelated mechanisms by which interspecific competition can set range limits along environmental gradients by preventing closely related species from coexisting.

Material and methods

Study region

Our study area is located in the Tropical Andes, home to the greatest concentration of terrestrial biodiversity on Earth (Myers et al. 2000). This 'mega' diversity is well illustrated by birds. There are ~800 resident bird species occur within our study site – the Manu Transect, a single ~30 km Amazon-to-Andes gradient in southeastern Peru – more than breed across the entirety of North America (Sibley 2000, Walker et al. 2006). Increased levels of biodiversity along tropical mountain slopes arise because high species richness within single elevational zones (alpha-diversity) is coupled with substantial species turnover between elevational zones (beta-diversity). Two examples illustrate the dramatic species turnover along this Manu Transect. First, despite a regional species pool of ~800 resident species, there are only eight species found in both lowland (< 500 m) and high elevation (> 3000 m) forests (Walker et al. 2006). Second, although this transect spans more than 3000 m of elevation, the average bird species inhabits only around one-third of the gradient [elevational breadth = 932 ± 555 m, mean ± standard deviation; n = 799 resident species, data from (Walker et al. 2006), omitting non-breeding visitors, species occurring at only a single
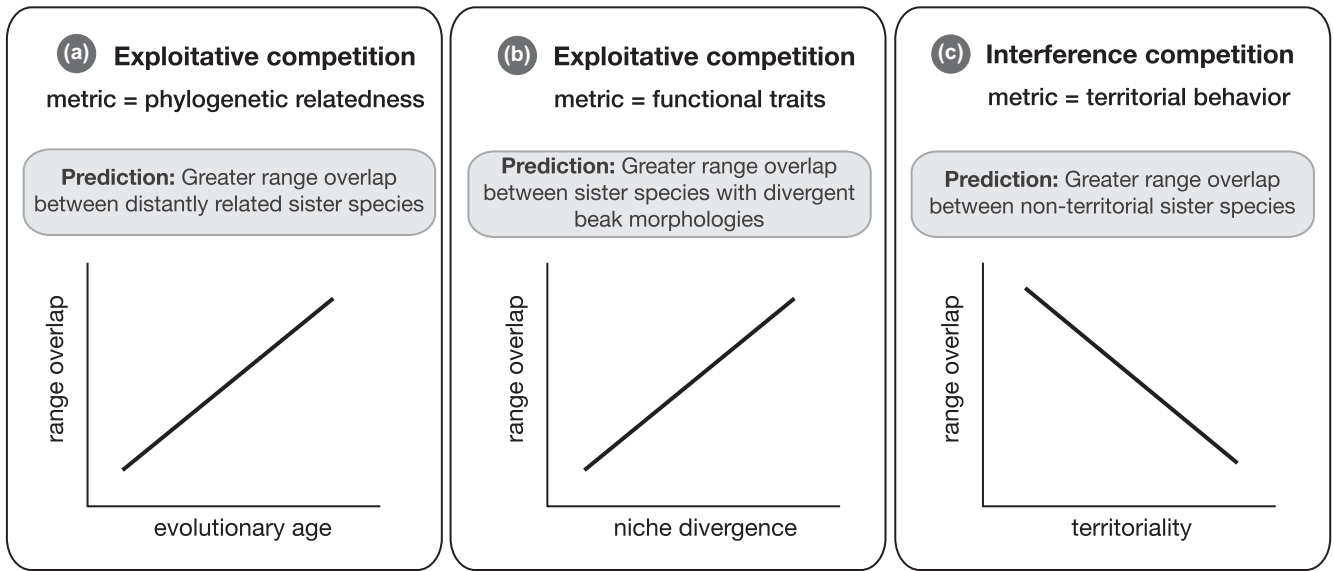
Figure 1. Hypotheses and predictions for patterns of coexistence in sister pairs distributed across an elevational gradient. We tested the hypothesis that exploitative competition influences patterns of coexistence using (a) evolutionary age (divergence time) and (b) divergence in an important functional trait (beak divergence), and the hypothesis that interference competition influences patterns of coexistence using (c) a behavioral trait (territoriality).

elevation, species that do not occur along the Manu Transect, and species that live only in agricultural or otherwise highly-modified habitats].

Elevational specialization, in conjunction with high species richness, provides the raw material for our comparative analysis of how competition between closely related species may influence range limits and patterns of coexistence along the Manu Transect. We investigated this question by 1) defining the set of bird species found along the Manu Transect as the regional species pool; 2) using species-level molecular phylogenies to define 'sister pairs' – two species that are each others' closest relatives – within this regional species pool; 3) measuring evolutionary and ecological variables for each sister pair; and 4) testing the predictions of three hypotheses that attempt to explain why some sister pairs overlap in elevational range along the transect while others do not (Table 1).

Defining sister pairs

For our baseline regional species pool, we used a published list of birds recorded in the Manu region (n = 851; Walker et al. 2006). Following Pigot et al. (2016), we removed all

non-breeding migrants, all species known from only a single record or elevation, any species not occurring along the best sampled transect (the Manu Transect, sometimes termed the 'Manu Road'), and species that live only in agricultural or otherwise highly-modified habitats. This resulted in a final list of 799 species (Supplementary material Appendix 1 Dataset A). We then scoured the literature to find species-level molecular phylogenies of groups that contain species found along the Manu Transect (see Supplementary material Appendix 1 Dataset A for groups for which we found species-level molecular phylogenies). We restricted our dataset to sister pairs where at least one species is an upland species with a low elevation limit > 400 m, to avoid the inclusion of sister pairs where both species are restricted to lowland Amazonian forest. We did not include lowland sister pairs for two reasons. First, we were interested in why some sister pairs overlap in elevational range while others do not, and lowland sister pairs would all be classified as having complete elevational overlap following our methodology. Second, the lowlands extend far into Amazonia, covering a much larger area than the elevational gradient we studied. This raises the problem that coexistence within the lowlands tells us little about spatial coexistence; lowland-lowland sister pairs may coexist or segregate spatially within the lowlands (e.g. one species inhabits riverine forest and the other terra firme forest).

We used molecular phylogenies to define 101 'sister pairs' – two species found along the Manu Transect that are each other's closest relatives within the Manu Transect assemblage (Supplementary material Appendix 1 Dataset B). In addition to defining sister pairs using molecular phylogenies, we included 17 sister pairs on the basis that they were the only members of their genus present along the Manu Transect

Table 1. Parameter estimates with standard errors for fixed effects for univariate regression models to predict elevational range overlap of sister pairs.

Model	Parameter	Estimate	SE	p-value
Beak divergence	Intercept	0.33	0.053	
	Beak divergence	0.26	0.13	0.042
Evolutionary age	Intercept	0.54	0.085	
	Evolutionary age	−0.020	0.015	0.18
Territoriality	Intercept	0.71	0.10	
	Territoriality score	−0.15	0.044	0.0013

(Supplementary material Appendix 1 Dataset B). All results are unchanged when analyzing only the 101 sister pairs included based on molecular phylogenies. Our approach parallels the common usage of 'sister pairs' in comparative evolutionary studies (Weir and Lawson 2015). Here we follow previous studies (Tobias et al. 2010) in defining sister taxa in the context of the study community. Thus, while some of these pairs of 'community sisters' are not each other's closest relatives at global scales, they are each other's closest relatives within the regional species pool.

Measuring coexistence

We quantified coexistence as the elevational range overlap between sister pairs. We defined species' elevational distributions along the Manu Transect using a single published dataset (Walker et al. 2006). This dataset provides elevational limits between 250 and 4000 m. However, most very high elevation species living along the Manu Transect are coded in this dataset as having an upper elevational limit of 3500 m when in reality they occur up to and often above 4000 m. We therefore standardized the upper elevation limit from 3500 m to 4000 m for species that inhabit high elevation puna habitats in this area, using a regional field guide (Schulenberg et al. 2010) and our observations from the field (Supplementary material Appendix 1 Dataset A). We made these changes to increase accuracy of the distributional dataset; all results remain unchanged when using the original elevational limits reported by Walker et al. (2006). We calculated elevational overlap as the percentage of the elevational distribution of the species with the smaller elevational range that overlapped with the larger-ranged species (following Freeman 2015). Thus, sister pairs with non-overlapping elevational ranges had an overlap score of 0, while sister pairs where the range of the smaller-ranged taxa is entirely subsumed within the larger-ranged species had an overlap score of 1. Sister pairs in our dataset varied in the extent of their elevational overlap: 42 sister pairs had zero elevational overlap; 24 had complete elevational overlap; and 50 had intermediate values. We consider sister pairs with overlapping elevational ranges to 'coexist', following the evolutionary ecology literature focused on understanding range limits and spatial variation in species richness (Pigot et al. 2018). We note that this usage differs from the concept of 'stable coexistence' in the theoretical ecology literature, which refers to species' ability to have a positive long-term growth rate when at low density at a particular site (HilleRisLambers et al. 2012).

Evolutionary and ecological traits

We defined three evolutionary and ecological metrics for the 118 sister pairs. First, we calculated beak divergence as the Euclidian distance between species in beak morphospace, following Pigot and Tobias (2013). Briefly, we made linear measurements (in mm) of four traits – bill length

of the culmen, bill length measured from the nares, bill depth and bill width – from multiple individuals of each species (mean = 10.55 individuals/species, range = 2–107). Measurements were taken from individual birds mist-netted in the field along the Manu Transect, and from specimens stored in museum collections (Trisos et al. 2014, Pigot et al. 2016). We took the log of each of the four traits and conducted a principal component analysis (PCA) to generate independent axes of variation in beak morphology. The first two principal components explained nearly the entirety of variation, and were related to overall beak size (PC1, 75.96% of variation) and shape (PC2, 21.20% of variation). We do not present a distinct analysis on body mass divergence in the main text because our analysis of beak morphology incorporates both differences in size and in shape (body mass divergence is unrelated to elevational overlap, Supplementary material Appendix 1 Fig. A1).

Second, we calculated divergence times, an estimate of the amount of time (in millions of years) that has elapsed since the two species last shared a common ancestor. We calculated divergence times from dated molecular phylogenies or, when these were not available, by extracting divergence times from figures of dated trees using WebPlotDigitizer (Rohatgi 2017). Some molecular phylogenies provided topologies that sufficed to define sister pairs, but did not present dated trees, which are necessary to determine divergence times. In total, we were able to calculate divergence times for most but not all (85 out of 118) sister pairs.

Third, we quantified territoriality using a recently published global dataset that classified intraspecific territorial defense of all bird species (Tobias et al. 2016). This dataset assigns species to one of three categories: species that do not defend territories (score = 1), species that are weakly or seasonally territorial (score = 2), and species that defend year-round territories (score = 3). See Tobias et al. (2016) for further details on the justification and definition of these categories, and data sources. Because territorial strategies are evolutionarily conserved, most species within a sister pair had identical territoriality scores (36, 32 and 34 sister pairs were designated with scores 1, 2 and 3, respectively). A small number of sister pairs were comprised of constituent taxa with territoriality scores of 1 and 2 (n = 3), or territoriality scores of 2 and 3 (n = 13). In these cases we measured territoriality of the sister pair as the average of the two scores. We coded territoriality score as numeric; results do not change if territoriality score is instead coded as a factor.

Last, we note that the size of species' elevational ranges influences the probability of elevational overlap. For example, if non-territorial species had broader elevational distributions than territorial species, then our null expectation would be for non-territorial species to have greater elevational overlap. This is not the case in our dataset. For the 236 species in our sister pair analysis (two species from 118 sister pairs), elevational range sizes were similar across different territorial scores (mean elevational range of 1158, 1194 and 1012 m for

territoriality scores of 1, 2 and 3, respectively; Supplementary material Appendix 1 Fig. A2). In addition, we report that apart from a few outliers, beak divergence was not related to territoriality score (Supplementary material Appendix 1 Fig. A3), indicating that these two metrics can be considered independent predictor variables.

Statistical analysis

We conducted all statistical analyses in R (R Development Core Team). We tested our hypotheses (Table 1) by fitting three distinct univariate linear models with elevational overlap as the response variable. We fitted two models to test the importance of exploitative competition in our dataset: a model with beak divergence as the predictor variable, and a model with divergence time as the predictor variable. We also fitted a model with territorial score as the predictor variable to evaluate whether interference competition might explain variation in coexistence in our dataset. We assessed the relative support of the three different univariate models by rerunning univariate models for only the 85 sister pairs for which we had complete information and using AIC model selection (which requires competing models to be fit to the same dataset). We ran 1) ordinary least squares regression models in order to use AIC model selection, and also 2) generalized linear models with family = quasibinomial (link = 'logit') to better approximate the error structure of our data. Last, we also fitted a multiple regression for the 85 sister pairs for which we had complete information, with beak divergence, divergence time and territoriality score as fixed effects.

We tested the influence of phylogenetic non-independence on our data by fitting a phylogenetic generalized least squares (PGLS) multiple regression using the 'ape' package (Paradis et al. 2004). The response variable in this model was elevational overlap and fixed effects were territoriality score, divergence time and beak divergence. We estimated

evolutionary relationships using a maximum clade credibility tree (implemented in TreeAnnotator; Rambaut and Drummond 2016) based on 1000 trees downloaded from birdtree.org (Hackett backbone, genetic only; Jetz et al. 2012), and estimated Pagel's λ using maximum likelihood. Note that the 'traits' in this model (elevational overlap, territoriality score, divergence time and beak divergence) are interactions between two closely related species (the sister pair). In order to run the PGLS, we coded these traits as belonging to one species in the sister pair. That is, we used a tree with 76 tips, one for each sister pair with complete data that was present in the Jetz genetic only tree (nine sister pairs in our dataset with complete data were not present in the Jetz genetic only tree).

Data deposition

Results

We report three main results. First, evolutionary age was not associated with coexistence (Fig. 2a, Table 1). Second, divergence in a resource acquisition trait was minimally related to elevational overlap. We found little support for the prediction that species with different beak morphology were more likely to have overlapping elevational distributions compared to species with similar morphologies (Table 1). The marginal statistical significance between beak divergence and elevational overlap we report (p = 0.042; Table 1) entirely disappears when we exclude two outlier sister pairs with high values of both beak divergence and elevational overlap (p = 0.31 after removing the two points in the furthest upper right of Fig. 2b). We therefore do not consider this result to be robust. Third, and in contrast, we
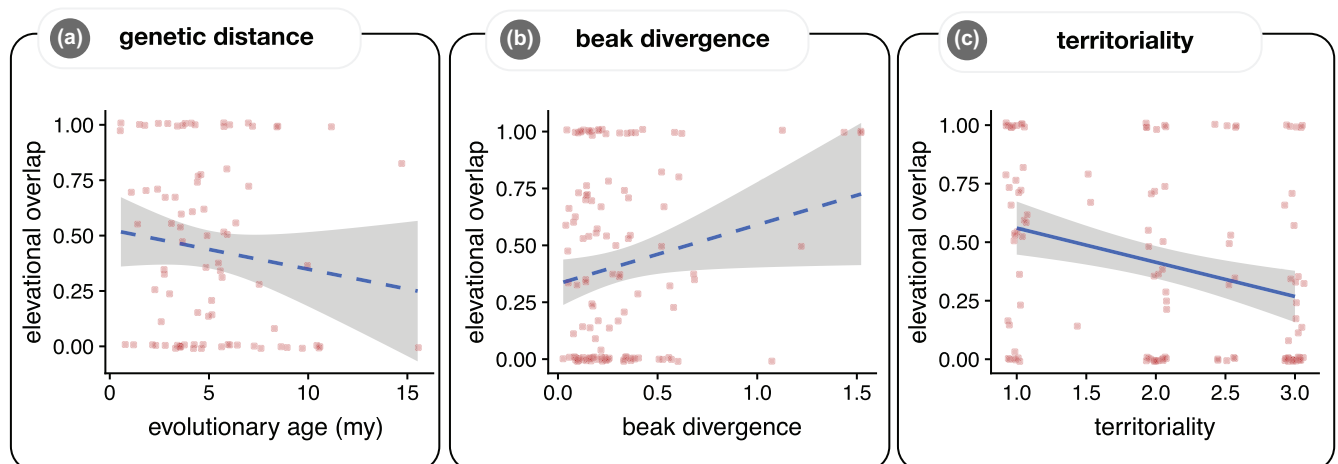

Figure 2. The relationship between elevational range overlap of sister pairs and (a) genetic distance, (b) beak divergence and (c) territoriality. Best-fit regression lines from univariate regression models are plotted in blue (significant = solid line, non-significant = dashed line) with 95% confidence interval shaded in gray. Data are jittered to improve clarity.

found support for the hypothesis that behavior shapes species' elevational ranges: Sister pairs where both taxa defend year-round territories had much lower elevational overlap than did pairs with weak or absent territoriality (Fig. 2c, Table 1, see also Fig. 3 for a case example). In the univariate regression model, estimated elevational range overlap was more than twice as large for sister pairs that do not hold territories compared to species that defend year-round territories (estimated range overlaps = 0.55 versus 0.26, respectively). When analyzing the data subset with complete information (85 sister pairs), the univariate model with territoriality score was the best supported (Supplementary material Appendix 1 Table A1, note that the evolutionary age model also receives high support), and territoriality score was the mostsignificant predictor in a multiple regression model (Supplementary material Appendix 1 Table A2, note that the estimate for evolutionary age in this subset is negative, contrary to the expectations presented in Fig. 1). Last, our results are robust to both modeling approaches (Supplementary material Appendix 1 Table A3) and phylogenetic non-independence of sister pairs (Supplementary material Appendix 1 Table A4).

Discussion

Our main finding is that patterns of range overlap in a diverse Andean avifauna are associated with behavioral traits rather than with metrics of evolutionary and morphological (beak) similarity. Specifically, we find that range overlap is predicted neither by beak divergence nor evolutionary age, but rather by strength of territoriality – closely related species that defend intraspecific year-round territories tend to live in different elevational zones with minimal overlap, while species that do not defend intraspecific territories generally overlap in elevational distribution. This general pattern is illustrated by the distributions of sister pairs within two sister genera of flycatchers that differ in territorial behavior, *Mionectes* and *Leptopogon* (Fig. 3). We interpret these findings as evidence that patterns of range limitation across an entire bird assemblage appear to be determined more by interference competition than by exploitative competition.

We are at present unable to decisively demonstrate the mechanistic link by which increased intraspecific territorial behavior leads to reduced range overlap. We hypothesize that the most likely mechanism explaining this pattern is that territorial species often defend their home range against heterospecifics (that tend to be close relatives and ecological competitors), and that interspecific territoriality reduces elevational range overlap between competing species. Consistent with this viewpoint, several case examples have demonstrated interspecific territoriality that appears to prevent coexistence between montane species, explaining why related species sometimes 'replace' one another along mountain slopes (Jankowski et al. 2010, Pasch et al. 2013, Freeman et al. 2016).

In contrast, we find little evidence that evolutionary or morphological similarity is related to patterns of coexistence. Hence, limiting similarity (MacArthur and Levins 1967) appears to be weak to absent, at least when considering certain traits (beak morphology and evolutionary age) at the spatial grain of elevational distributions along a single gradient. We emphasize that the strength of limiting similarity is likely scale-dependent. For example, a previous study
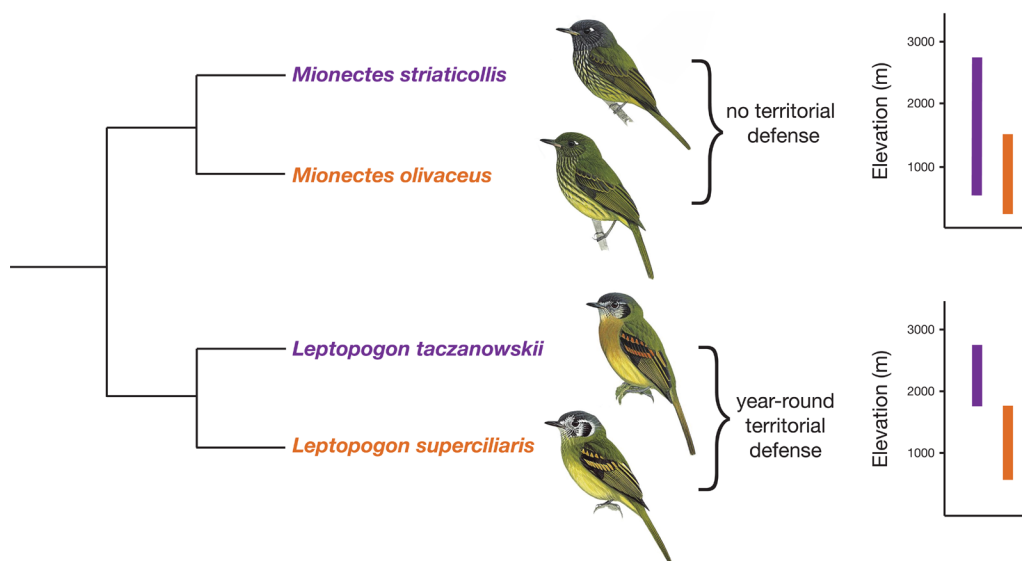

Figure 3. A case example illustrating general patterns. *Mionectes* and *Leptopogon* are sister genera (Miller et al. 2008) that contain morphologically similar sister pairs. *Mionectes* do not defend territories and have broad elevational range overlap, while *Leptopogon* defend year-round territories and sharply replace each other at 1800 m. *Mionectes striaticollis* and *olivaceus* are sister taxa (Miller et al. 2008), while *Leptopogon taczanowskii* and *superciliaris* are sister taxa within the Manu avifauna (Winger and Bates 2015). Illustrations reproduced by permission of Lynx Edicions.

also found little signal of limiting similarity when comparing avian assemblages across elevations at our study site using the same traits we studied (Trisos et al. 2014). However, the key result of this previous study was that morphologically and evolutionary similar taxa seldom overlapped in territories – that is, limiting similarity is strong, but only at the small spatial scale of individual territories (Trisos et al. 2014). At slightly larger scales, limiting similarity also appears to structure bird assemblages in small forest fragments (Ulrich et al. 2018). These findings are consistent with the view that competitive effects are strongest at small spatial scales and decline with increasing spatial scale (Bullock et al. 2000, Cavender-Bares et al. 2006, Lovette and Hochachka 2006). However, we note that the dimensions of the niche which we quantified in our study are rather simplistic (e.g. we did not include diet, foraging strata, foraging strategy or microhabitat), and that patterns consistent with limiting similarity have sometimes been found at biogeographic scales (Pigot and Tobias 2013).

The robustness of our interpretations depends on the datasets we use to quantify species-pairs traits as well as the validity of our metrics of competition. The Manu Transect is the only Andean elevational gradient with comprehensive distributional information we are aware of. Still, while we argue the datasets we used in this analysis are appropriate, they are imperfect, adding noise (but not bias) to our analyses. In particular, the morphological dataset we analyze is state-of-the-art for a diverse system, which gives us confidence in our result that beak divergence is minimally related to elevational overlap. Turning to the validity of our metrics of competition, we note that the metrics we use as proxies for intensity of exploitative competition – beak morphology and evolutionary similarity – are widely used in the literature, but have been challenged. For example, evolutionary relatedness may not be a reliable proxy for the intensity of competition (Mayfield and Levine 2010), casting doubt on the usefulness of phylogenetic relationships as a proxy for intensity of exploitative competition. In contrast, the assumption that species with similar resource acquisition traits tend to compete more strongly for resources is likely to generally hold. For example, the link between similarity in beak morphology and competition for resources in birds is particularly well supported (Grant and Grant 2006, Ryan et al. 2007). Perhaps our most important assumption is that the intensity of intraspecific territorial behavior is a useful metric of interference competition between species. It seems reasonable that intraspecific territorial behavior is a precondition for interspecific territorial behavior – we are not aware of cases where a species defends its territory against heterospecifics but not conspecifics. Nevertheless, further work measuring interspecific territorial defense in the field in tropical taxa would be necessary to test this assumption. Last, we note that much variation in range overlap among sister pairs remains unexplained – territoriality is not the only variable explaining observed patterns of elevational range overlap.

Implications and speculation

To what degree can our results, which apply to a particular assemblage along a particular transect, be generalized to other geographic arenas? We suggest that our primary result – the importance of behavioral interactions to understanding patterns of coexistence – is likely to be of general importance. Interspecific defense of territories has been commonly noted in intraspecifically territorial birds in both the tropics and temperate zone (Garcia 1983, Robinson and Terborgh 1995, Seddon and Tobias 2010, Losin et al. 2016), as well as in a variety of other vertebrate groups (Griffis and Jaeger 1998, Pasch et al. 2013). Hence, we hypothesize that territorial interactions may often limit coexistence of close relatives within certain environments (e.g. in this study, different elevational zones). Supporting this conjecture, previously documented cases of interspecific territoriality are often associated with specialization to different microhabitats (Garcia 1983, Robinson and Terborgh 1995, Seddon and Tobias 2010). We emphasize that our study is conducted at a rather coarse grain – because we do not have territory-level information for species, we treat elevational zones as homogenous landscapes. Hence, we almost certainly underreport the importance of interference competition in shaping species' distributions. Related species commonly partition habitats within a single elevational zone (e.g. forest versus bamboo, see Tobias et al. 2010), but, because we ignore habitat heterogeneity, our analysis classifies such cases as complete range overlap.

Further research should investigate whether the common observation that closely related sympatric taxa specialize on different habitats may be partially driven by behavioral interactions. In addition, broader scale analyses are needed to test for latitudinal trends in the importance of behavioral interactions in explaining geographical distributions. We suspect that behavioral interactions may be a more important driver of distributions in the tropics compared to the temperate zone. This is in part because species interactions are thought to be stronger in the tropics (Schemske et al. 2009), but also because many tropical species are year-round residents that defend permanent territories in diverse communities containing greater numbers of potential ecological competitors (Tobias et al. 2016).

Conclusions

Our results indicate that behavioral interactions can be generally important in setting elevational range limits and preventing coexistence of closely related species in a diverse assemblage. This finding adds weight to recent evidence that territorial behavior plays a significant role in structuring tropical montane bird communities (Ulrich et al. 2018). In contrast, we find little evidence that limiting similarity shapes range limits at the scale of elevational transects, in line with some previous studies (Trisos et al. 2014). By showing that territorial system can explain patterns of range limitation better than morphological traits linked to resource acquisition,

our study provides some support for MacArthur's (1972) claim that 'behavior reduces a chaotic scramble to an orderly contest'. The idea that behavior represents a key dimension of the niche is far from new (Hutchinson 1959), but this insight tends to be either overlooked or relegated to a footnote by macroecologists and biogeographers. Our findings suggest that, on the contrary, behavioral traits linked to interference competition need to be explicitly considered as potential factors explaining large-scale patterns of diversity and coexistence.

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Supplementary material (available online as Appendix ecog-04606 at <www.ecography.org/appendix/ecog-04606>). Appendix 1.