Limits to elevational distributions in two species of emberizine finches: disentangling the role of interspecific competition, autoecology, and geographic variation in the environment

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When species' elevational ranges are wider where putative competitors are absent, researchers have concluded that interspecific competition influences elevational distributions. This overlooks the distinction between factors that limit distributions directly and factors that only influence organisms indirectly through covarying regulators or resources. Because elevation affects organisms indirectly, testing whether competition influences elevational ranges relies on the heretofore untested assumption that the relationship between elevation and factors influencing organisms directly is similar across geography. Focusing on *Buarremon* brush-finches (Aves: Emberizidae), a group in which distributions represent one of the best examples of the potential role of competition limiting elevational ranges, we show that when distributions are compared along axes of climatic variation, some patterns of elevational range variation do appear to be consistent with predictions of the hypothesis that release from competition underlies expanded elevational ranges in allopatry. However, other patterns of expanded elevational ranges in the absence of putative competitors are better explained by hypothesis related to species' autoecology and geographic variation in the environment. This latter finding cautions against using elevation uncritically as a dimension of ecological niches, and suggests that classical examples of interspecific competition may need re-evaluation.

The idea that interspecific interactions impose limits to the distribution of organisms, from local patterns of habitat use to geographic ranges at regional scales, is pervasive in ecology (MacArthur 1972). In particular, the influence of interspecific competition on distributions is explicitly embodied in some definitions of the ecological niche (Pulliam 2000), a central concept of ecological theory (Chase and Leibold 2003). According to niche theory, competitive interactions constrain species to occupy a limited portion – the realized niche – of the full spectrum of conditions under which they could maintain populations – the fundamental niche (Hutchinson 1957).

Testing whether interspecific competition limits species' distributions is challenging because experiments cannot be conducted over landscape to regional scales. Thus, researchers often rely on "natural experiments", comparing species' ranges in the presence and absence of putative competitors. When distributions along ecological gradients are narrower in the presence of competitors, competitive displacement in sympatry or competitive release in allopatry are inferred. In particular, because species often occur over wider ranges of elevation where potential competitors are absent, interspecific competition is thought to underlie parapatric distributions along elevational gradients (Lack and Southern 1949, Diamond 1970, 1973, Terborgh and Weske 1975, Mayr and Diamond 1976, Remsen and Cardiff 1990, Remsen and Graves 1995).

Many studies on the role competition plays limiting geographic ranges compare the position of species along gradients of a single variable selected from among all those that may constrain their distributions. This narrow focus may be misleading, particularly when

the variables examined are not those that directly limit species' ranges, but rather surrogates for factors that may covary with them in complex ways. One such surrogate is elevation, which in itself does not limit species' ranges along montane gradients. Instead, these are governed by regulators or resources (Austin and Smith 1989) that covary with elevation (temperature, partial oxygen pressure, food availability) and impose limits to organisms directly. As is typical for indirect gradients as defined by niche theory (Austin and Smith 1989, Huston 1994, Austin 1999, 2002), the relationship between many of these factors and elevation is context-dependent. For example, although temperature declines with increasing elevation, this relationship varies with latitude, the mass of mountains, and the orientation of mountains with respect to prevailing winds. Therefore, "elevation" may pose different challenges to the performance of organisms and thus to the persistence of populations in different areas (Janzen 1967, Ghalambor et al. 2006). Consequently, the inference that expanded elevational ranges in allopatry reflect a release from competition relies on the assumption that environments located at the same elevations in sympatry and allopatry are equivalent in terms of factors that affect organisms directly. Because previous studies have not tested this assumption explicitly, one cannot rule out the hypothesis that expanded elevational ranges in allopatry reflect the response of organisms to geographic variation in the way in which elevation covaries with environmental conditions.

Here, we present a refined approach to study the role of interspecific competition in elevational replacements that considers niche differentiation with reference to climatic variables that likely impose limits to geographic ranges along montane slopes in a more direct fashion than elevation. We focus on *Buarremon* brush-finches (Aves, Emberizidae), whose elevational distributions are strongly believed to be influenced by competition (Remsen and Graves 1995). By assessing patterns of niche differentiation using ecological niche modeling (Guisan and Thuiller 2005, Elith et al. 2006) and multivariate analyses of climate data, we confirm that some patterns of variation in elevational distributions are consistent with predictions of the hypothesis of competitive release in allopatry. However, we also find that patterns seemingly consistent with this hypothesis have alternative, more parsimonious, explanations.

Study system

The chestnut-capped *Buarremon brunneinucha* and stripe-headed *B. torquatus* brush-finches are common understory passerine birds occurring in Neotropical montane forests. Although these species are not as closely related as traditional taxonomy would suggest (Cadena et al. 2007), they have parapatric elevational distributions where they co-occur, and *B. torquatus* occurs over much of the montane gradient where *B. brunneinucha* is naturally absent, suggesting the range of *B. torquatus* is limited by competition in sympatry (Remsen and Graves 1995). In contrast, the elevational ranges of *B. brunneinucha* are not wider in allopatry, yet, on average, populations occur at higher elevations in sympatry (Cadena 2007). Because the shift to higher elevations in sympatry is consistent across areas where *B. brunneinucha* is replaced at high elevations, replaced at low elevations, and sandwiched by populations of *B. torquatus*, it is not likely associated with competitive displacement, but rather with an increased abundance of sites at higher elevations where the two species are sympatric (Cadena 2007).

Although Remsen and Graves (1995) and Cadena (2007) argued that elevational distributions in different areas are roughly comparable to each other in terms of conditions likely affecting the distributions of brush-finches directly, they did not formally address this assumption. In fact, there are compelling reasons why elevational ranges may not be readily comparable across areas as a result of varying environmental conditions. Consider the three regions where populations of *B. torquatus* have expanded elevational ranges in the absence of *B. brunneinucha*: 1) an ocean-facing slope of an isolated mountain massif that rises from dry lowlands in close proximity to the Caribbean Ocean and is exposed directly to trade winds coming from the north (the northern slope of the Sierra Nevada de Santa Marta in northern Colombia; Pérez Preciado 1984), 2) an area with strong seasonality whose climate is affected strongly by the Pacific Ocean, from which it is separated by a narrow stretch of xeric lowlands (the western slope of the Andes in southwestern Ecuador and northwestern Peru; Best and Kessler 1995), and 3) the most southerly latitudes at which *B. torquatus* occurs, where habitats differ from those of the tropical Andes (the Andes of Bolivia and Argentina; Fjeldså and Krabbe 1990). Environmental conditions, such as temperature and precipitation (hence vegetation; Holdridge 1967), may differ markedly between these mountain slopes and others, such as those on the eastern versant of the Andes. Likewise, on average, the populations of *B. brunneinucha* occurring in the absence of *B. torquatus* (Mexico through central Costa Rica) are located at more northerly latitudes than those occurring in sympatry.

Hypotheses and predictions

Two hypotheses may account for wider elevational ranges where potential competitors are absent. First,

range expansions may reflect that the environmental conditions over which species can maintain populations occur over a broader range of elevations in areas of allopatry. We refer to this hypothesis as that of autoecology because it implies that species occur in similar environments throughout their ranges, tracking their ecological requirements. Alternatively, expanded distributions in allopatry may reflect release from competitors. These hypotheses are testable by examining the environmental conditions under which species occur in sympatry and allopatry (Anderson et al. 2002). If wider elevational ranges in allopatry reflect autoecology, then environmental conditions of sites occupied in these areas should resemble those of sites located in areas where closely allied populations co-occur with potential competitors. In contrast, competitive release predicts that the environmental space occupied should be wider in allopatric populations in comparison to populations potentially constrained by competition in sympatry. Furthermore, the expansion in environmental space in allopatry should result from the occupation of niche space that the putative competitor occupies in sympatry.

Materials and methods

Locality data

We compiled primary occurrence data for *B. torquatus* and *B. brunneinucha* based on museum specimens, publications, records provided by several ornithologists, and observations we made in the field. We entered data into a Geographical Information System (GIS; ArcGIS 9.0, ESRI) by georeferencing all available localities using a variety of gazetteers (e.g. Paynter 1997; GEOnet Names Server: <http://earth-info.nga.mil/gns/html/index.html>). As a first step to verify georeferencing accuracy, we relocated points that mapped to obviously incorrect countries, provinces, or geographic regions. We then cross-checked each point for correspondence between the elevation recorded in specimen labels or measured in the field and the elevation indicated by a digital elevation model with a 1×1 km resolution (Shuttle Radar Topography Mission; <http://www.jpl.nasa.gov/srtm>). Georeferences for which both sources of elevation data differed by ≤ 100 m were left unchanged. Cases revealing discrepancies were either corrected by moving points to the nearest site matching the elevation on the primary data if this site was within $2-3$ km of the original georeference, georeferenced again and re-checked, or discarded if accurate coordinates could not be obtained. For localities lacking elevation data, most of which were in Mexico, we extracted the elevation from the digital model and excluded all those extending beyond the known elevation range of each taxon in the region (Howell and Webb 1995). Although this approach does not guarantee records will be mapped with maximum accuracy, it is conservative in that localities representing conditions extending beyond those known to be experienced by populations are not considered. Finally, to reduce pseudoreplication (although this procedure does not eliminate the non-independence of localities owing to spatial autocorrelation in climate data), we randomly excluded records of the same taxon located within 1 km of one another, because this was the highest resolution for the digital elevation model and climate data (see below). The final database consisted of 342 and 350 localities for *B. brunneinucha* and *B. torquatus*, respectively. For each locality, we recorded whether it was located in areas of sympatry or areas of allopatry based on distribution maps and compilations of locality data (Remsen and Graves 1995, Ridgely et al. 2005, this study). The areas from where one of the species is absent have been extensively sampled using techniques likely to lead to its detection as revealed by the existence of multiple records of the other species, suggesting absences over broad areas are real, and not artifacts of incomplete sampling (Anderson 2003).

Ecological niche modeling

We examined niche differentiation based on 19 climate variables on a 30 arc-second resolution grid obtained from WorldClim (Hijmans et al. 2005; Table 1). These variables reflect annual trends (e.g. mean annual temperature), seasonality (e.g. isothermality), and extreme values (e.g. temperature of the coldest month) in conditions thought to be important in limiting species' distributions directly. However, the influence of some WorldClim variables on distributions is likely indirect (e.g. through their influence on regulators, resources, or other organisms; Austin 2002). Nonetheless, we believe this climatic data set represents a closer approximation to ecological niches than elevation, which can only influence distributions indirectly.

We used principal components analysis (PCA) to reduce the 19 WorldClim variables to uncorrelated, independent variables that we then employed to construct niche models. We recorded the value of each WorldClim variable at 100 000 points placed randomly across all countries where *Buarremon* species occur, and used these data to conduct a PCA in SAS ver. 9.1 (SAS Inst., Cary, NC). Using the eigenvector coefficients obtained, we created GIS layers covering the study region for each principal component using the raster calculator in ArcMap. Four of these layers were then used for modeling because their eigenvalues exceeded those predicted by a broken-stick model (Peres-Neto et al. 2003) and explained most (91%) of

Table 1. Climatic variables obtained from WorldClim employed in environmental characterizations of the distributions of *Buarremon* brush-finches. For each variable, its loadings on each of the four axes following varimax rotation resulting from the two principal components analyses (PCA) conducted are shown. The regional PCA was based on data from 100 000 randomly placed points and was used only to reduce the variables used for modeling (i.e. climate surfaces corresponding to each of the first four axes were used as independent variables to construct DOMAIN models; see Methods). The locality-based PCA used all sites of known occurrence of *Buarremon* and forms the basis for Fig. 5 and related discussions. For detailed descriptions of how each original climate variable was calculated and how the interpolated climate surfaces were created, see Hijmans et al. (2005) and <www.wordclim.org>.

Variable	Regional PCA				Locality-based PCA			
	PC1	PC2	PC3	PC4	PC1	PC2	PC3	PC4
Annual mean temperature	0.911	−0.278	0.114	−0.053	0.169	0.010	−0.046	0.026
Mean diurnal temperature range	0.029	0.600	0.020	0.737	−0.011	0.211	−0.040	0.086
Isothermality	0.288	−0.269	0.491	0.741	0.013	−0.221	−0.070	−0.004
Temperature seasonality	−0.122	0.898	−0.215	−0.084	0.003	0.290	0.002	0.124
Maximum temperature of warmest month	0.949	0.247	0.058	0.141	0.133	0.421	−0.041	0.167
Minimum temperature of coldest month	0.768	−0.515	0.258	0.025	0.165	−0.460	−0.028	−0.145
Annual temperature range	−0.063	0.891	−0.166	0.303	0.000	0.000	0.000	0.000
Mean temperature of wettest quarter	0.925	−0.011	0.089	0.117	0.158	0.076	−0.047	0.053
Mean temperature of driest quarter	0.796	−0.406	0.208	0.124	0.166	−0.075	−0.034	−0.012
Mean temperature of warmest quarter	0.977	0.081	0.116	0.083	0.156	0.073	−0.037	0.046
Mean temperature of coldest quarter	0.810	−0.464	0.215	0.116	0.167	−0.096	−0.040	−0.028
Annual precipitation	0.279	−0.391	0.507	−0.131	−0.036	0.020	0.230	0.041
Precipitation of wettest month	0.342	−0.401	0.273	0.108	−0.057	−0.030	0.333	−0.163
Precipitation of driest month	0.201	−0.112	0.919	0.055	0.007	0.118	−0.030	0.361
Precipitation seasonality	0.135	0.096	−0.271	0.902	−0.023	−0.054	0.180	−0.372
Precipitation of wettest quarter	0.316	−0.425	0.261	0.025	−0.057	−0.025	0.331	−0.153
Precipitation of driest quarter	0.166	−0.196	0.865	−0.172	0.005	0.104	−0.022	0.349
Precipitation of warmest quarter	0.237	−0.237	0.490	−0.015	−0.040	0.081	0.218	0.043
Precipitation of coldest quarter	0.222	−0.301	0.421	−0.092	0.014	0.004	0.038	0.184

the climatic variation (Table 1). In addition, because locality data for some populations were limited (≤ 20 records), including more variables may have resulted in model over-fitting.

Using the GIS layers corresponding to the four composite environmental variables created using PCA, we modeled ecological niches of various populations (see below) employing the DOMAIN algorithm (Carpenter et al. 1993) in DIVA-GIS (<http://www.diva-gis.org>). We chose this algorithm because its output can be readily interpreted as a measurement of overall environmental similarity to sites where a taxon is known to occur, and is thus consistent with niche theory (Hill and Binford 2002). DOMAIN assigns each grid cell a multivariate distance (Gower 1971) to the closest site (i.e. in evironmental space) in which the taxon being modeled occurs. Specifically, the algorithm sums the standardized distances across environmental variables between each grid cell and the environmentally most similar grid cell where the taxon is known to occur. Environmental distance at each grid cell is then subtracted from 1 and multiplied by 100 to provide similarity values ranging from 0 to 100, where values approaching 100 indicate increasing similarity to sites of known occurrence. At a similarity score of 100, two sites have identical values for all four composite environmental variables. Many studies employing DOMAIN to predict distributions consider

sites to be suitable when receiving scores ≥ 95. Because our focus is not on predicting potential distributions, but rather on describing ecological similarity between sites, we follow this convention only when presenting the geographic projection of niche models or for display purposes in graphs; we treat DOMAIN scores as a continuous variable indicating environmental similarity to sites of known occurrence.

We tested the predictions of autoecology and ecological release for the four cases of elevational range expansions or shifts in allopatry mentioned above: populations of *B. torquatus* from the Sierra Nevada de Santa Marta, the Pacific Andean slope, and the Andes of Bolivia and Argentina (see distribution map in Remsen and Graves 1995), and populations of *B. brunneinucha* from Mexico to central Costa Rica. For each of these "target" populations, we constructed two different niche models that served to evaluate the predictions of each hypothesis, one based on localities of conspecific populations occurring in sympatry with the putative competitor, and one on localities of the putative competitor from areas of sympatry (Table 2). All models included the four composite environmental variables created using PCA. For each case, we projected both of these models onto geographic space, and then recorded the DOMAIN score on each model at all the points of occurrence of the target population. This resulted in data sets in which localities of target

Table 2. Populations of *Buarremon* with expanded or shifted elevational ranges in areas where competitors are absent and populations used to construct models that allowed testing the hypotheses of autoecology and competitive release in each case.

Target populations with expanded or shifted elevational range in allopatry	Population or taxa modeled	
	Autoecology hypothesis	Competitive release hypothesis
B. torquatus basilicus Sierra Nevada de Santa Marta (N Colombia)	*B. t. perijanus* and *B. t. larensis*[1] (NE Colombia – NW Venezuela)	*B. brunneinucha* in sympatry with *B. torquatus* (central Costa Rica – Peru)
B. torquatus nigrifrons Pacific slope of the Andes (Ecuador – Peru)	*B. t. assimilis*[2] (Ecuador – Peru)	*B. brunneinucha* in sympatry with *B. torquatus* (central Costa Rica – Peru)
B. t. torquatus, *B. t. fimbriatus,* and *B. t borelli* (Bolivia – Argentina)	*B. torquatus* east Andean slope (Colombia – Peru)	*B. brunneinucha* in sympatry with *B. torquatus* (central Costa Rica – Peru)
B. brunneinucha, several subspecies (Mexico – central Costa Rica)	*B. brunneinucha* in sympatry with *B. torquatus* (central Costa Rica – Peru)	*B. torquatus* in sympatry with *B. brunneinucha*[3] (central Costa Rica – Peru)

[1]These populations occur in sympatry with *B. brunneinucha* and are those in closest geographic proximity to the Sierra Nevada de Santa Marta. Also, mitochondrial sequence data (Cadena et al. 2007) indicate *B. t. perijanus* is the sister taxon of *B. t. basilicus*.
[2]This taxon is very closely allied to *B. t. nigrifrons* (i.e. they are each others closest relatives and have not attained reciprocal monophyly in mtDNA; Cadena et al. 2007) and occurs in sympatry with *B. brunneinucha*.
[3]The populations of *B. torquatus* considered are only those that occur in sympatry with *B. brunneinucha* in the region: *costaricensis, tacarcunae, atricapillus, assimilis, larensis, perijanus, phaeopleurus,* and *poliophrys* (*basilicus, phygas, nigrifrons, torquatus, fimbriatus* and *borelli* are not included).

populations were associated with two scores, one indicating environmental similarity to sites occupied by a population of the same species occurring in sympatry with the putative competitor, and one indicating similarity to sites occupied by the putative competitor. We compared these scores for each target population using paired t-tests: significantly higher scores on the model constructed for the conspecific population (i.e. higher ecological similarity to the conspecific than to the heterospecific population) would support autoecology and higher scores for the heterospecific one would support competitive release. This test was somewhat inconclusive for the case involving populations of *B. brunneinucha* in sympatry and allopatry because the differences in scores between models, despite being statistically significant, appeared to be of little biological significance (see Results). Therefore, we also projected the model based on data from localities in allopatry onto the area of sympatry, where we recorded the score at each occurrence site. This allowed us to further evaluate the two hypotheses by examining the scores of sites in sympatry based on the model constructed with data from allopatry and vice versa. If the shifted range towards higher elevations in sympatry reflects competitive displacement, then sites at higher elevations in sympatry should receive lower scores in the model based on data from allopatry (a regression between elevation and model scores would have a negative slope), and sites at lower elevations in allopatry should receive lower scores in the model based on data from sympatry (the regression would have a positive slope). Alternatively, if the shift reflects autoecology, there should be no relation between elevation and model scores.

Multivariate analysis

The projection of niche models onto geographic space allows one to determine whether environments where allopatric populations occur resemble more closely those occupied by individuals of the same species elsewhere or those occupied by the species that is a putative competitor. However, models do not indicate which climatic variables contribute most to overall assessments of environmental differences and similarities. We pursued this question examining climatic variation using PCA. Instead of using the layers created for niche modeling, we conducted a new PCA with varimax rotation considering only climatic data (i.e. the 19 WorldClim variables) recorded at localities where *B. torquatus* and *B. brunneinucha* occur. This allowed us to visualize variation in ecological niches by plotting the scores of each of the localities along axes of environmental variation.

Results

Buarremon torquatus in the Sierra Nevada de Santa Marta

The elevational range of the population of *B. torquatus* occurring in the Sierra Nevada de Santa Marta (*B. t. basilicus*) is one of the widest among all populations of *B. torquatus*, ranging from ca 500 to 3000 m. Niche modeling shows that all of the localities where *B. t. basilicus* occurs are climatically similar to sites where *B. brunneinucha* is found elsewhere: all localities received higher DOMAIN similarity scores on the model constructed for *B. brunneinucha* (mean score $\pm$

SD: 98.3 ± 1.9) than on the model based on localities of *B. t. perijanus* and *B. t. larensis* (79.4 ± 15.1) despite the fact that the latter populations occur in close proximity to Santa Marta. Mean similarity scores on the *B. brunneinucha* model were significantly higher (t = 5.62, 17 DF, p < 0.0001), and were always > 95%, whereas none of the scores on the *B. torquatus* model reached this value (Fig. 1). These results are consistent with the hypothesis that *B. t. basilicus* occurs over a broad elevational range filling ecological space occupied elsewhere by *B. brunneinucha* (competitive release), not by tracking conditions under which conspecific populations occur elsewhere (autoecology).

Buarremon torquatus on the Pacific Andean slope

On the Pacific slope of the Andes of southern Ecuador and northwestern Peru, *B. torquatus nigrifrons* occurs over a wide range of elevations, and extends to lowland areas that its sister taxon (*B. t. assimilis*) never occupies. Similarity scores recorded at *B. t. nigrifrons* localities were significantly higher (t = 5.4, 36 DF, p < 0.0001) on the model constructed based on *B. brunneinucha* localities (96.2 ± 4.0) than on the model based on records of *B. t. assimilis* from Colombia, Ecuador, and Peru (88.9 ± 9.2). Moreover, the environmental conditions at all eight localities of *B. t. nigrifrons* below the lower elevational limit of *B. t. assimilis* were more similar to those of sites occupied by *B. brunneinucha* where it co-occurs with *B. torquatus* than to sites occupied by *B. t. assimilis* (Fig. 2). Again, these data indicate that the expanded elevational range of

B. t. nigrifrons may reflect release from competition with *B. brunneinucha*.

Buarremon torquatus in Bolivia and Argentina

Localities where *B. torquatus* occurs in Bolivia and Argentina are environmentally more similar to sites occupied elsewhere by *B. brunneinucha* (90.1 ± 7.1) than to sites occupied by *B. torquatus* along the eastern slope of the Andes where it co-occurs with *B. brunneinucha* (83.1 ± 11.4). Although mean similarity scores differed significantly between models (t = 10.7, 83 DF, p < 0.001), scores on both models were generally low in comparison to those obtained for other target populations. This suggested that neither autoecology nor ecological release might be the best explanation for the expanded elevational range of *B. torquatus* in the region, which prompted us to examine the data in more detail. First, because environments in northern Bolivia are rather different from those in southern Bolivia and Argentina (see below), we conducted an additional paired t-test in which we compared scores on DOMAIN models using as a target population only those *B. torquatus* localities from northern Bolivia (14.6°–16.9°S). This was further justified because if competitive release in fact exists, it is more likely to be evident in this area because it is immediately south of the southern limit of the distribution of *B. brunneinucha*. Although localities of *B. torquatus* in this region tended to be more similar environmentally to sites occupied in areas of sympatry by *B. brunneinucha* (97.9 ± 0.54) than to sites occupied
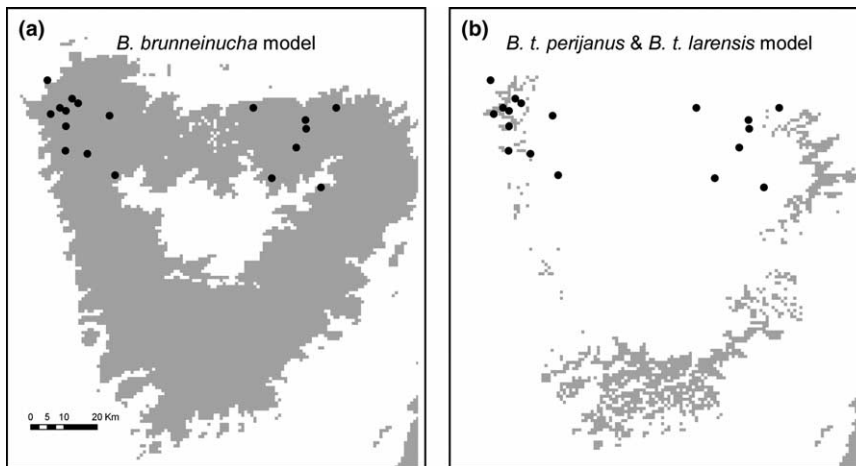

Fig. 1. Geographic projections onto the Sierra Nevada de Santa Marta of ecological niche models constructed for (a) *B. brunneinucha* and (b) populations of *B. torquatus basilicus* occurring in the Serranía de Perijá and the eastern Andes of northeast Colombia and west Venezuela. Points are the localities of known occurrence of *B. torquatus* in the region and shaded areas indicate grid cells receiving DOMAIN scores ≥95%. Models classify extensive areas as suitable for *B. brunneinucha*, but only limited areas for the *B. torquatus* taxa, and all localities match sites of predicted presence of *B. brunneinucha*, not of *B. torquatus*, supporting the hypothesis of competitive release.
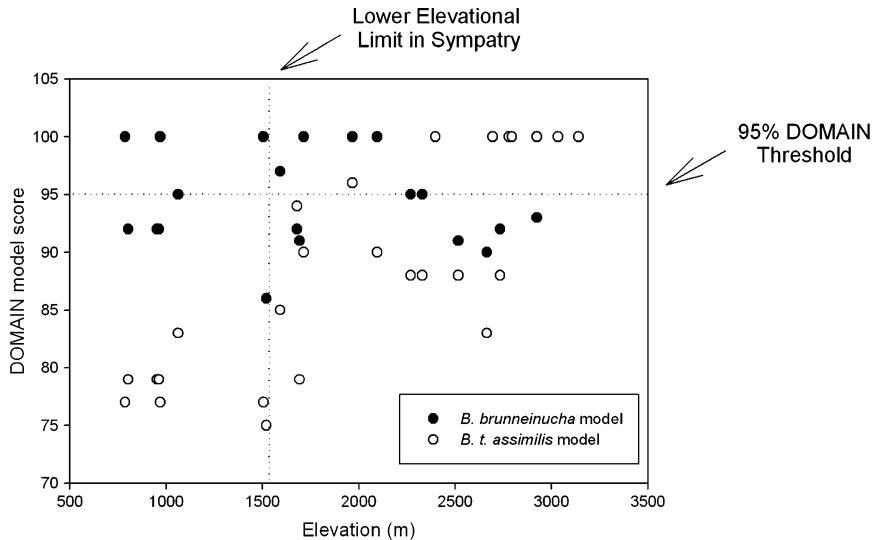
Fig. 2. DOMAIN similarity scores obtained by overlaying localities of known occurrence of *B. torquatus nigrifrons* on the Pacific slope of the Andes of southern Ecuador and northern Peru onto ecological niche models constructed based on locality data for *B. brunneinucha* (black dots) and *B. torquatus assimilis*, its sister taxon occurring through Colombia, Ecuador, and northern Peru (white dots). The vertical dotted line shows the lower elevational limit of *B. t. assimilis* where it co-occurs with *B. brunneinucha*, and the horizontal line indicates the 95% threshold of environmental similarity. Note that DOMAIN scores for all localities of *B. t. nigrifrons* under the lower elevational limit of *B. t. assimilis* in sympatry are higher on the model based on locality data from *B. brunneinucha*. Some localities at higher elevations received equal scores on both models; in these cases points overlap, but only those on the *B. t. assimilis* model are shown.

by *B. torquatus* where sympatric with *B. brunneinucha* (95.5 ± 1.67), this was not statistically significant (t = 1.60, 14 DF, p = 0.131), suggesting there is no support for the hypothesis of competitive release.

Furthermore, niche models indicate that the low-elevation environments to which *B. torquatus* expands in southern Bolivia and Argentina are distinct from those occupied by *B. brunneinucha* in areas where both species co-occur. Of a total of 32 localities in which *B. torquatus* occurs at elevations below those known from areas where it co-occurs with *B. brunneinucha*, only four correspond to sites that DOMAIN classified as climatically suitable for the latter species (scores ≥95%), all of which are located at elevations within 100 m of the lowest record of *B. torquatus* in areas of sympatry (Fig. 3a). This result is insensitive to the cutoff value applied to discriminate between suitable and unsuitable sites for *B. brunneinucha*: there is a strong negative correlation between elevation and model scores (Fig. 3b). Low environmental similarity to sites of known occurrence in this region is also observed based on the niche model constructed with data from the rest of the range of *B. torquatus* (not shown). In sum, the expansion of *B. torquatus* in Bolivia and Argentina to low elevations cannot be explained satisfactorily by the hypotheses of autoecology or competitive release because the environments to which it expands are not similar to those occupied by

either *B. brunneinucha* or *B. torquatus* in areas of sympatry.

Buarremon brunneinucha in allopatry and sympatry

Sites where *B. brunneinucha* occurs in allopatry from *B. torquatus* are significantly more similar (t = 6.84, 115 DF, p < 0.0001) to sites occupied by this species in areas where it is sympatric with *B. torquatus* (95.8 ± 3.7) than to the sites that *B. torquatus* occupies in areas of sympatry (93.9 ± 4.6). However, differences in scores between the two models do not seem as biologically compelling as in other cases, suggesting this comparison is insufficient to favor the hypothesis of autoecology, which we explore further below.

Buarremon brunneinucha occurs in similar environments irrespective of the presence of *B. torquatus*: most localities in areas of allopatry received scores ≥95% on the model constructed with data from sympatry, and vice versa (Fig. 4a). Although the model from allopatry performed less well in characterizing the environments the species occupies in sympatry (scores under 90% were more frequent), all localities from sympatry receiving low scores on the model from allopatry occur at comparatively low elevations (Fig. 4b), which is contrary to the pattern expected if the shift to higher elevations in sympatry were the result of competition.
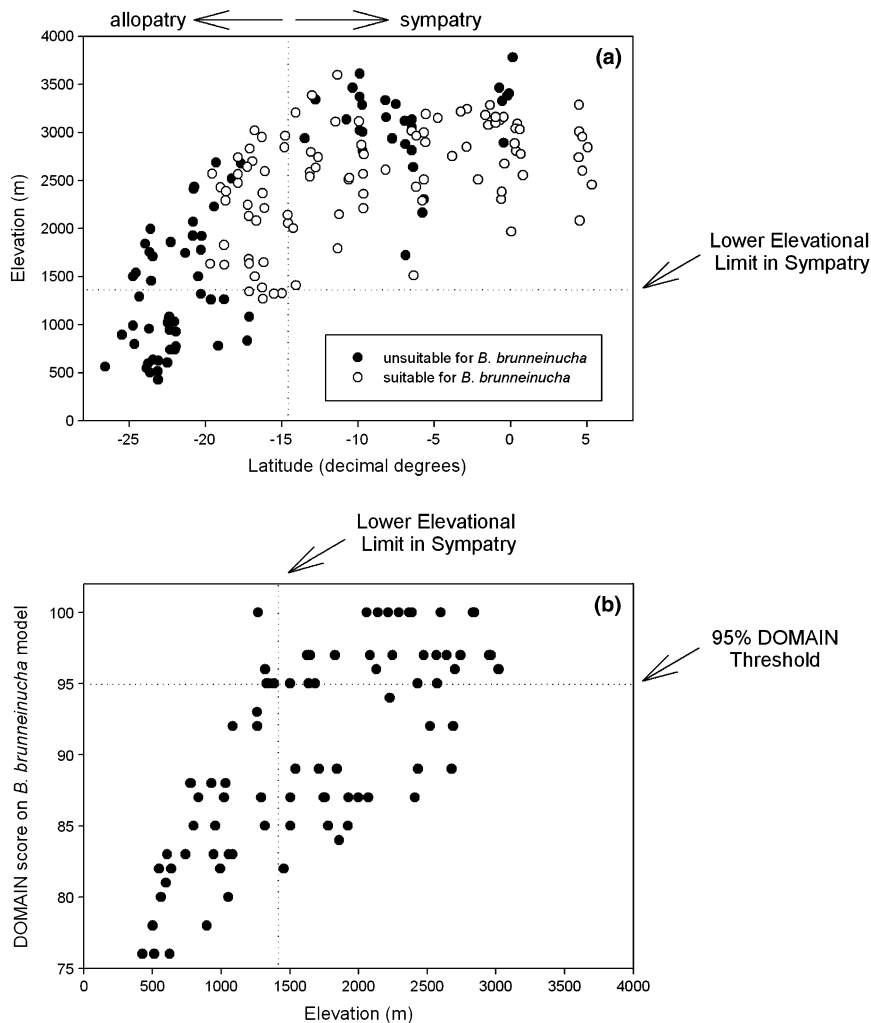
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Fig. 3. (a) Elevational distribution of *B. torquatus* with respect to latitude along the eastern slope of the Andes, from Colombia to northern Argentina. The vertical line indicates the approximate latitude marking the southern limit of the distribution of *B. brunneinucha* and the horizontal line the lowest elevation at which *B. torquatus* is known to occur in this slope in areas where it co-occurs with *B. brunneinucha*. Dots are colored according to whether they are above (white) or below (black) the 95% environmental similarity threshold according to the ecological niche model constructed based on locality data for *B. brunneinucha*. Note that all sites at which *B. torquatus* occurs at high latitudes and low elevations are classified as unsuitable for *B. brunneinucha* by the model. (b) Positive relationship between elevation and environmental similarity to sites where *B. brunneinucha* occurs for records of *B. torquatus* from the eastern slope of the Andes, indicating its expansion to lower elevations does not reflect the occupation of environments occupied by its potential competitor in areas of sympatry.

Moreover, the slopes of regressions between elevation and model scores are not different from zero in either sympatry ($0.002s \pm 0.001$ SE) or allopatry (0.001 ± 0.001), implying that the shift to higher elevations in sympatry is fully consistent with autoecology.

Multivariate analysis

PCA reduced the variation in climate across the ranges of brush-finches to a few axes of variation (Table 1), allowing us to distinguish sets of potentially limiting climatic variables that correlate with elevation from sets that do not. Although elevation was not included in the analyses, scores along the first principal component, which accounted for 38% of the climatic variation, correlate tightly with elevation. High scores along this axis indicate high values for annual mean temperature, maximum temperature of the warmest month, minimum temperature of the coldest month, and mean temperatures of the wettest, driest, warmest, and coldest quarters. The second axis accounted for 33% of the
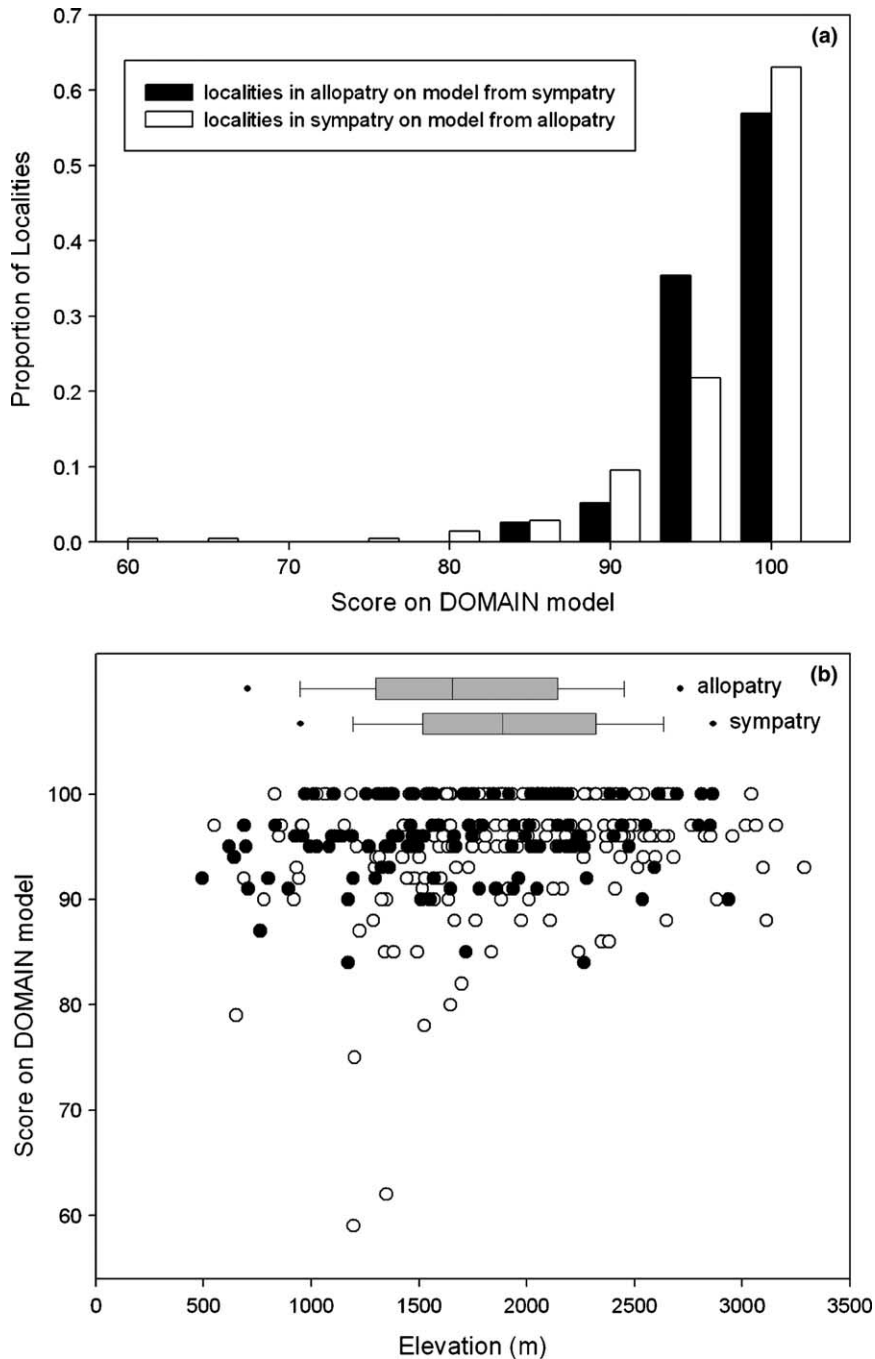
Fig. 4. (a) Frequency distribution of similarity scores of records of *B. brunneinucha* from areas of sympatry to models constructed based on data from allopatry (white bars) and vice versa (black bars). Note that in both cases the majority of records are at or above 95%, indicating the environments occupied by the species in sympatry and allopatry are similar. However, sites receiving scores ≤90% are more common for localities in sympatry. (b) Lack of relationship between elevation and the environmental similarity of records of *B. brunneinucha* from areas of sympatry to models constructed based on data from allopatry (white dots) and vice versa (black dots). Box plots show the shift in distribution to higher elevations in sympatry.

variation, and has a close correspondence with variables that covary with latitude. High scores reflect high values of mean diurnal range in temperature, temperature seasonality, and temperature annual range, and low values of isothermality. The third axis accounted for 13% of the variation; high values reflect high annual

precipitation, precipitation during the wettest month, and precipitation during the wettest and warmest quarters. Finally, the fourth axis explained 7% of the variation; scores correlate positively with precipitation during the driest month, driest quarter, and coldest quarter, and negatively with precipitation seasonality.

Based on scores along the first principal component, populations of *B. torquatus* occurring in Bolivia and Argentina indeed occupy environments that are intermediate between those occupied by lowland and highland populations of *B. torquatus* and resemble closely those occupied by *B. brunneinucha* (Fig. 5a, c). However, the second principal component indicates that sites occupied by *B. torquatus* are characterized by environmental conditions that are not experienced by *B. brunneinucha* anywhere on the part of its range where it co-occurs with *B. torquatus* (Fig. 5c). In addition, the

range of variation in climatic variables that correlate with elevation (PC 1) over which Bolivian and Argentinean populations occur is not nearly as wide in comparison to that of other populations as a cursory examination of elevational distributions would suggest (contrast elevation range and PC 1 range in Fig. 5e and f). Also, the range of environmental conditions in which these populations occur is limited compared to others in other dimensions of climatic space (PC 3 and 4, Fig. 5b).

The discrepancy in the mean elevational distributions of *B. brunneinucha* in sympatry and allopatry becomes less pronounced when these populations are plotted along the first climatic principal component (Fig. 5e, f). The reduced ability of the model from allopatry to establish environmental suitability in sympatry likely results from changing climatic conditions with latitude; localities receiving lower scores on
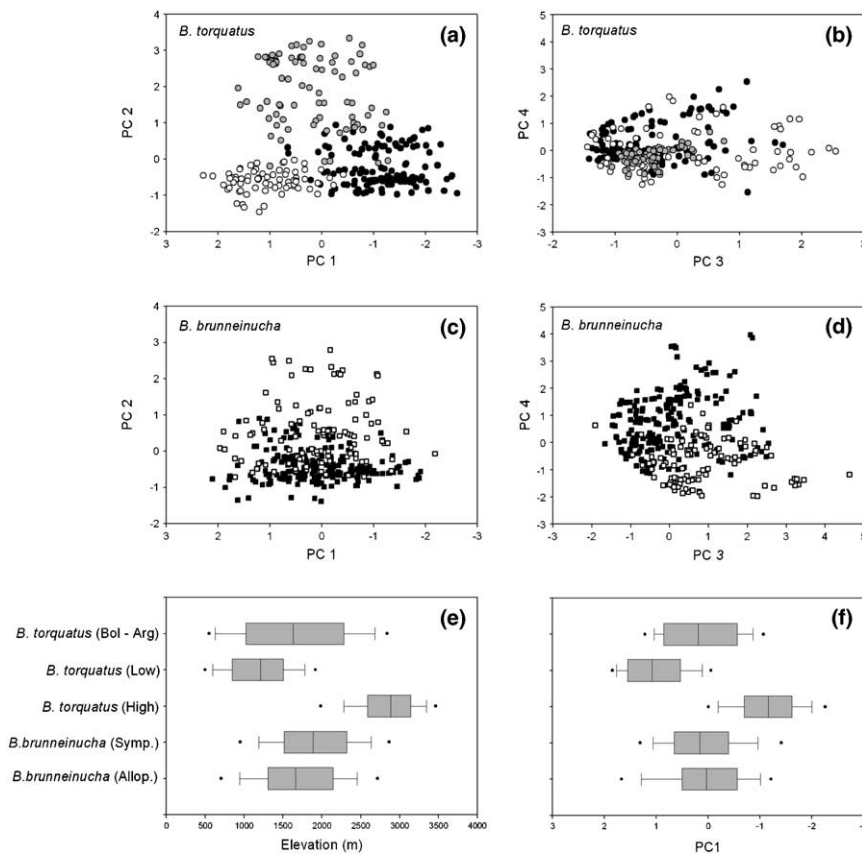

Fig. 5. Results of principal components analyses of climatic variation observed at localities of occurrence of *B. torquatus* and *B. brunneinucha.* Panels (a) through (d) show the positions in environmental space along the first four principal components of different populations (note that the scale of the first component has been inverted to indicate increasing elevations from left to right). In (a) and (b), grey circles correspond to localities of *B. torquatus* in Bolivia and Argentina, and white and black circles to localities of this species from areas where it replaces *B. brunneinucha* at low and high elevations, respectively. White and black squares in (c) and (d) are localities where *B. brunneinucha* occurs in allopatry and sympatry with *B. torquatus,* respectively. Panels (e) and (f) illustrate that differences among populations in elevational ranges are more pronounced than differences in the actual range of climatic conditions that correlate with elevation (i.e. principal component 1) under which these populations occur.

the model (Fig. 4b) are those with higher values along the second principal component (Fig. 5c), which correlates tightly with latitude.

Discussion

Our analyses support the predictions of competitive release for some populations of *Buarremon* occurring in allopatry from competitors but not for others. In the Sierra Nevada de Santa Marta and the Pacific Andean slope of southern Ecuador and Peru, the elevational expansion of *B. torquatus* indeed results in the occupation of climatic niche space that *B. brunneinucha* occupies in areas of coexistence, and is not consistent with tracking of geographic variation in the elevations at which favored conditions occur. In contrast, attributing the wide elevational range of *B. torquatus* in Bolivia and Argentina to release from competition with *B. brunneinucha* is untenable because the environments to which the species expands are not equivalent to those occupied by its potential competitor in areas of sympatry. Finally, the shift towards higher elevations of populations of *B. brunneinucha* occurring in sympatry with *B. torquatus* is not likely a consequence of the presence of the competitor, but is consistent with autoecology. In combination with differences in the availability of sites at different elevations between areas of sympatry and allopatry (Cadena 2007), this suggests that the elevational range of *B. brunneinucha* was most likely not influenced by *B. torquatus* as it encountered this species following its range expansion from northern Central America (Cadena et al. 2007). This leads us to reject the hypothesis that elevational distribtions in *Buarremon* arose as a consequence of reciprocal contractions in the ranges of both species resulting from competition, a mechanism thought to underlie elevational replacements in many areas (Diamond 1973). However, because our analyses are consistent with predictions of ecological release for two populations of *B. torquatus* occurring in areas where *B. brunneinucha* is absent, we cannot reject the hypothesis that ranges of *B. torquatus* are influenced by *B. brunneinucha* (i.e. asymmetric competition; Cadena 2007).

Remsen and Graves (1995) convincingly documented an almost perfect complementarity in the elevational distributions of *B. torquatus* and *B. brunneinucha*, with very limited overlap and almost no documented cases of sympatry. Our compilation of additional localities reveals that the overlap in elevational distributions is much greater than previously thought. For example, records of *B. brunneinucha* from the Colombian Andes range from ca 850 to 3280 m, whereas along the same slopes, those of *B. torquatus assimilis* range from ca 1850 to 3630 m and those of *B. t. atricapillus* from ca 670 to 2000 m. Indeed, at

many of the sites where we conducted fieldwork for this study (in Colombia, Costa Rica, and Peru) we found the two species in strict sympatry (e.g. captured them in the same mist nets on the same day), often at elevations where only one of them was expected based on the data presented by Remsen and Graves (1995). This does not imply that elevational replacements between the two species do not exist, but it indicates that part of the evidence for ecological incompatibility that led previous authors to propose a role for interspecific competition in limiting their distributions (Paynter 1978, Fjeldså and Krabbe 1990, Remsen and Graves 1995) is not as strong as it once seemed.

Our analyses show that considering environmental variables that likely limit species' distributions directly, or that at least are more proximate to relevant dimensions of ecological niches than elevation by itself, elevation may mean different things in different areas. Ecologists have long recognized that the relationship between elevation and climate varies with latitude (Janzen 1967), but we emphasize that the lack of consistent "meaning" for elevation need not involve variation in latitude nor manifest itself over broad spatial scales. For example, although there are many sites at the same elevations in the Sierra Nevada de Santa Marta and the adjacent Serranía de Perijá and the Andes of northeast Colombia and west Venezuela, the environments at these sites differ, as shown by the limited areas of high suitability identified for *B. t. perijanus* and *B. t. larensis* in Santa Marta (Fig. 1). That elevation may mean different things in different areas even over small scales implies that some classic examples of competitive displacement and release along elevational gradients (e.g. Diamond 1973, Terborgh and Weske 1975) may need re-evaluation.

A related issue is that the occurrence of a population over a wide elevational range need not imply that it occurs over a broader range of environmental conditions than a population with a more restricted elevational range. For example, although the elevational range of populations of *B. torquatus* in Bolivia and Argentina as a whole is wider than that of populations occurring in sympatry with *B. brunneinucha*, the differences in ecological amplitude among regions do not appear nearly as large when considered in terms of the climatic variables that correlate with elevation (PC 1, Fig. 5e, f). This most likely reflects that the elevational distribution of *B. torquatus* is not consistent through Bolivia and Argentina: with increasing latitudes, the range is displaced to lower elevations (Fig. 3a). Indeed, at any given latitude, the elevational range of *B. torquatus* is not any wider than that of populations occurring in sympatry with *B. brunneinucha*. Particularly, in contrast to Remsen and Graves (1995), with our expanded locality database we find no strong evidence of an expansion of the elevational range

of *B. torquatus* immediately south of the area where the distribution of *B. brunneinucha* drops off, which is what the hypothesis that competition limits elevational distributions would predict.

More generally, our analyses show that niche breadth along one axis of ecological differentiation may say little about niche breadth along other axes (contrast the large range of environmental conditions occupied by Bolivian-Argentinean populations along PC 1 and 2 and the narrow ranges along PC 3 and 4; Fig. 5). Therefore, although elevation is a valid surrogate for important ecological variation, it is uninformative about differentiation along niche axes that may be just as important descriptors of the ecology of populations. The implications are twofold. First, examining only elevation is insufficient to ascertain whether the expansion of elevational ranges of populations in allopatry results from occupying the environmental space that competitors occupy in sympatry. Second, the observation that populations occurring with and without competitors have similar elevational distributions does not imply that species do not impose limits to each other's ranges in areas where they come into contact. Elevation is perhaps the easiest dimension of niche space to examine, but there is no reason why ecological displacement cannot occur along direct climatic gradients uncorrelated with elevation (Melville 2002).

In describing the hypotheses that could account for expanded elevational ranges in the absence of competitors, we mentioned ecological release and autoecology. Our analyses reveal the importance of a third hypothesis: geographic variation in the realized environment (sensu Jackson and Overpeck 2000). Populations of *B. torquatus* occur over a wide elevational range in Bolivia and Argentina, but this entails the occupation of environments characterized by high values along principal component 2 (i.e. high mean diurnal range in temperature, temperature seasonality, and temperature annual range; low isothermality) that do not exist throughout the rest of the distribution range of this species. Thus, the wide elevational range of *B. torquatus* in the region cannot be explained on the basis of the hypotheses of autoecology or ecological release. Patterns such as this one may reflect either evolution of fundamental niches as populations encounter varying environmental conditions across their ranges (Holt 2003), or simply a more complete expression of realized niches that is not possible anywhere else owing to geographic variation in the environment; distinguishing these alternatives requires experiments (Kearney and Porter 2004, Kearney 2006). It follows that contrary to claims made in the literature (Peterson et al. 1999, Soberón and Peterson 2005), niche models do not approximate fundamental niches. In addition, we suggest that tests of ecological and evolutionary hypotheses about ecological niches across geography based on environmental data (Peterson et al. 1999, Anderson et al. 2002, Peterson and Holt 2003, Hoffmann 2005) should consider the combinations of conditions actually existing in different areas. For instance, Graham et al. (2004) concluded that most speciation events involve both geographic isolation and ecological differentiation because many sister species are allopatric and occur in climatically different environments (see also Kozak and Wiens 2006). Without information on whether similar environments in fact exist in allopatry, it is unclear whether the correlation between ecological divergence and speciation is causal, or rather a fortuitous byproduct of a correlation between geographic distance and environmental dissimilarity.

We have assumed that climate affects the distributions of populations along elevational transects through direct effects on the performance of organisms. This assumption has been well-established by functional studies (Porter et al. 2002, Navas 2003, Altshuler and Dudley 2006), implying that our approach is closer to characterizing ecological niches than that of studies that only consider elevation, which affects organisms only indirectly. However, climate influences elevational distributions indirectly as well. For example, temperature, precipitation, and evapotranspiration influence vegetation structure (Holdridge 1967), which in turn affects species' distributions. Just as the relationship between elevation and climate is context-dependent, elevation, climate, vegetation, and other factors influencing distributions are unlikely to covary equally everywhere. Therefore, geographic variation in elevational distributions may arise if organisms track niche dimensions that cannot be predicted precisely based on climate, a possibility that our analyses do not address. Nevertheless, this further illustrates the importance of distinguishing variables that affect species' distributions directly from those that do not, and cautions against using elevation uncritically as a dimension of ecological niches.

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