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Niche incumbency, dispersal limitation and climate shape geographical distributions in a species-rich island adaptive radiation

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ABSTRACT

Aim To test the role of climate, dispersal limitation and biotic interactions in limiting species' distributions within an island adaptive radiation by integrating species traits, phylogeny and estimates of dispersal cost into climate-based species distribution models.

Location Hispaniola.

Methods Focusing on 26 species of *Anolis* lizards, we used multivariate adaptive regression splines to evaluate the contribution of climate, species interactions, phylogenetic history and dispersal limitation to species distributional limits. For each species, we mapped the morphological similarity of congeners using traits of known ecological import and predicted that species would be less likely to occur in climatically suitable areas if they were inhabited by ecologically similar species. Dispersal limitation was incorporated by generating spatially explicit estimates of dispersal cost, based on inferred habitat suitability. We compared models including morphological similarity, dispersal cost, phylogeny and climate with climate-only models. Results were evaluated against a null model that conserved the spatial structure of species occurrences.

Results Climate had a dominant role in shaping species distributions. However, for over one-third of species we also found evidence consistent with supplemental effects of species interactions, i.e. ecological niche incumbency. These species were less likely to occur in climatically suitable areas inhabited by a morphologically similar species. Dispersal limitation also supplemented climatic limits in most species. These results were robust to co-variation with phylogeny and to comparison with our null model.

Conclusions These results suggest that, rather than act as mutually exclusive alternatives, multiple dimensions of the ecological niche, including climatic limits, biotic interactions and dispersal capacity, interact to shape species distributions and that local interactions can influence the broad-scale geography of species in a predictable way.

Keywords

Anolis, biotic interactions, competitive exclusion, dispersal barriers, ecological niche, lizards, range limits, realized niche, species distribution modelling, trait-based ecology.

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INTRODUCTION

The geographical distribution of a species reflects numerous factors acting at multiple scales, including climatic limits, dispersal limitation, microhabitat requirements and local biotic interactions (Pulliam, 2000; Soberón, 2007; Soberón & Nakamura, 2009). Although theory acknowledges a role for biotic interactions and dispersal barriers in limiting geographical distributions (Hutchinson, 1957; Soberón, 2007; Holt, 2009), recent empirical treatments have emphasized broad environmental (mostly climatic) variation. A role for other factors may be inferred when climate-based models fail, but explicit predictions based on alternative processes, such as species interactions, are rarely tested (but see Araújo & Luoto, 2007; Glor & Warren, 2011). Here, we assemble models that incorporate multiple dimensions of a species' ecological niche, including regional variation in climate, landscape-scale dispersal barriers and trait-mediated local interactions. We use these models to test predictions of how these factors jointly determine distributional limits within a species-rich adaptive radiation.

Negative local interactions among similar species can lead to ecological niche incumbency, where a species is prevented from expanding its range into an otherwise suitable area because of an incumbent species with a similar niche (Williams, 1965; MacArthur, 1972; Glor & Warren, 2011). Despite its theoretical plausibility, the role of niche incumbency in limiting distributions remains uncertain because of the difficulty in identifying species that are likely to negatively interact and in detecting the effect of these interactions at broad spatial scales (Araújo & Luoto, 2007; Soberón, 2007; Gotelli *et al.*, 2010). One potential solution is to focus on species' traits (McGill *et al.*, 2006). The strength of trait-based approaches lies in the fact that how species interact with their environments is a function of their phenotypes. For example, beak shape and size determine resource use efficiency, fitness and competitive outcomes for Galápagos finches (Grant & Grant, 2010). Thus, the similarity of

traits important for microhabitat use and resource partitioning among species can be used as a geographically quantifiable proxy of the potential for niche incumbency; species more similar in inferred resource use are more likely to experience negative competitive interactions that preclude coexistence (MacArthur & Levins, 1967). Using this principle, we quantify how traits are distributed geographically and incorporate this trait landscape into species distribution models. We predict that models will infer lower suitability for the focal species at locations where a morphologically similar species occurs (Fig. 1) even if the abiotic conditions are suitable.

Species may be absent from environmentally suitable regions for reasons other than niche incumbency. In particular, the inhospitality of the intervening habitat matrix may prevent species from reaching all suitable areas (Pulliam, 2000; Soberón, 2007; Graham *et al.*, 2010; Glor & Warren, 2011). Although methods to evaluate dispersal barriers exist, they are applicable only to species pairs with well defined, nearly abutting, range boundaries (Kozak & Wiens, 2006; Glor & Warren, 2011). Here, building on landscape genetic approaches (e.g. Wang *et al.*, 2008), we construct dispersal cost surfaces based on inferred climatic suitability. These estimate the difficulty of dispersing to a particular region (Ferrier *et al.*, 2007), which allows for a more nuanced quantification of dispersal limitation than simply classifying particular landscape features as dispersal barriers. We predict that species are less likely to occur in areas that are difficult to reach, i.e. with high dispersal costs, even if those areas are climatically suitable.

We tested the above predictions for 26 species of *Anolis* lizards on Hispaniola by comparing models that included climate, the trait landscape and estimated dispersal cost with traditional climate-only models. We also tested models that incorporated phylogenetic relatedness to account for possible confounding relationships with phylogeny. In particular, closely related species may not co-occur because their ranges have had insufficient time to expand after allopatric speciation (Barraclough &

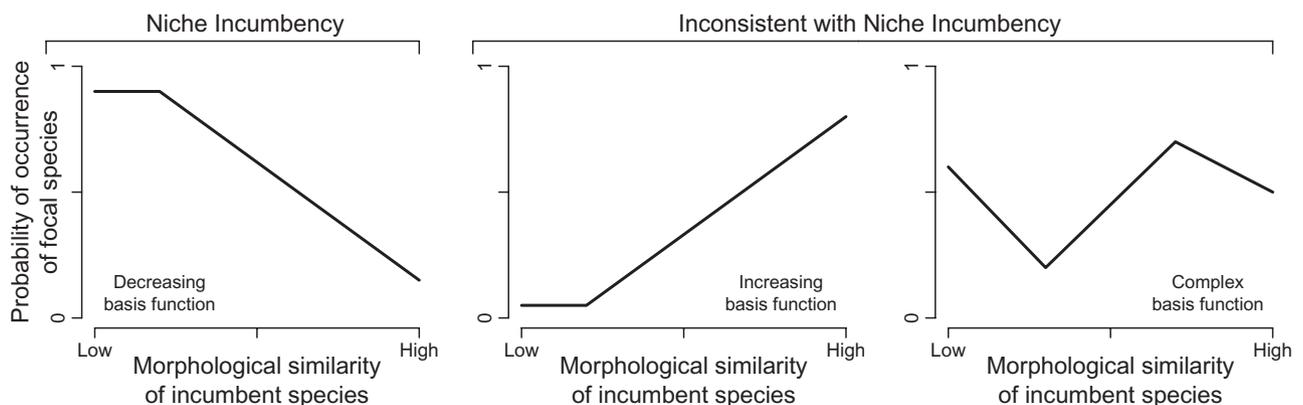


Figure 1 The predicted relationship between a species' probability of occurrence and its morphological similarity to species present at a locale (incumbent species) when niche incumbency does or does not limit species distributions. Shown are examples of three possible basis function shapes (increasing, decreasing or complex) from multivariate adaptive regression spline (MARS) models that are consistent (left panel) or inconsistent (two right panels) with niche incumbency. Basis functions were considered complex if they did not increase or decrease for > 80% of their range.

Vogler, 2000; but see Losos & Glor, 2003). Hispaniolan anoles are especially suited for these tests because: (1) they are species-rich and ecologically diverse (Losos, 2009; Algar & Losos, 2011); (2) they are well represented in museum collections and have been densely sampled (see Fig. S1 in Supporting Information); (3) there is substantial climatic variation on Hispaniola and anoles are known to utilize a variety of climes (Glor *et al.*, 2003); and (4) there is substantial evidence that species interactions are predictably mediated by morphological traits. In particular, an extensive history of experimental and field studies has demonstrated a strong link between anole morphology and microhabitat use. Species that use similar microhabitats (e.g. trunk, trunk-crown, grass-bush) have similar morphologies that have been linked to improved performance in those habitats (reviewed in Losos, 2009). Furthermore, sympatric species that use similar microhabitats can differ in body size, which has been linked to prey-size partitioning (Rand & Williams, 1969; Schoener, 1970; Losos, 2009). Thus, we expect the strongest interactions to occur between similarly sized species that use the same microhabitats, i.e. the most morphologically similar species. We predict that, even after accounting for climate, modelled suitability for a species will be negatively related to the morphological similarity of incumbent species and also to the estimated difficulty (cost) of dispersing to a locale. We test these predictions for 26 anole species and compare the results with a null model that assumes species occurrences are independent of climate, dispersal cost, phylogeny or niche incumbency.

METHODS

Species occurrence data

Species occurrences were obtained from HerpNet for 37 *Anolis* species on Hispaniola for which we also had morphological and phylogenetic information (<http://www.herpnet.org>). Species occurrences with ambiguous taxonomy were discarded. Species occurrences were checked for consistency with those in Schwartz & Henderson (1991) and checked for accuracy by R.E.G. and other experts. Localities from R.E.G.'s field series were also included. The accuracy of occurrences georeferenced from locality descriptions varies with the quality of the original description. To account for this, we combined occurrences from all 37 species and then merged points that were separated by less than 3000 m (the median georeferencing uncertainty reported by HerpNet). To merge occurrences, we successively discarded points based on the number of neighbours within a 3000-m radius, with the most highly connected points eliminated first. The final set of occurrences included 740 unique localities (Fig. S1).

Morphological and phylogenetic landscapes

We obtained morphological data from Mahler *et al.* (2010). Traits included body size and shape, head size and shape, limb traits, toe pad characteristics and tail length (Mahler *et al.*, 2010). We then used the first five principal components from a

phylogenetic principal component analysis (PCA) on these traits for nearly all Greater Antillean species to calculate the Euclidean trait distance among Hispaniolan species. Phylogenetic PCA is an adaptation of PCA that accounts for phylogenetic non-independence of trait data, assuming Brownian motion evolution (Revell, 2009). We used inverse Euclidean distance as a measure of similarity.

Next, we generated two morphological similarity landscapes for each species. Treating each of the 740 unique collection localities on Hispaniola in turn, we determined the most morphologically similar species (relative to the focal species) recorded at a locality and assigned its similarity to that locality. We refer to this as the MorphSim landscape. The second landscape (MorphNbr) was based on occurrences of the focal species' nearest neighbour in morphological space; localities where this species had been collected were given values equal to its similarity to the focal species; areas where it had not been collected were given values of zero.

To examine whether relationships between morphological similarity and occurrence could be due to phylogenetic relatedness, we repeated our analyses using landscapes generated using phylogenetic similarity. We used the maximum credibility clade tree based on the sample from the Bayesian posterior distribution of ultrametric trees described by Mahler *et al.* (2010). Similarity was quantified as the shared branch length among pairs of species. PhySim and PhyNbr landscapes were then calculated as described above for morphology. The PhyNbr landscape quantifies the distribution of each species' closest relative and thus can detect an effect of time-since-speciation on range overlap between sister species (assuming range dynamics are not too fast to obliterate the signal; Losos & Glor, 2003).

Climatic suitability and dispersal barriers

Quantifying dispersal barriers for a particular species required an estimate of habitat suitability. We estimated the climatic suitability across Hispaniola for each species by fitting a multivariate adaptive regression spline (MARS; Friedman, 1991; Elith & Leathwick, 2007; Rubidge *et al.*, 2011) using climate variables as predictors. We used MARS models, rather than alternative methods, to retain consistency with our full distribution models, which are explained below. Following Glor & Warren (2011), we accounted for high multicollinearity among climatic variables by performing a PCA on the 19 BIOCLIM variables from the WorldClim database (<http://www.worldclim.org>; Hijmans *et al.*, 2005) at 30 arcsec resolution. We retained the first six principal components, which explained 98.2% of the variance in climate across Hispaniola (Table S1). We fitted a MARS model for each species using target-group pseudo-absences, i.e. locations where other anole species had been collected but the focal species had not (Mateo *et al.*, 2010). We standardized prevalence across species by weighting presences and absences so that prevalence equalled 0.5 (Elith & Leathwick, 2007). MARS models did not include interactions and used a penalty of 2 (Leathwick *et al.*, 2005; Elith & Leathwick, 2007). After fitting, basis functions

were extracted and used as predictors in a generalized linear model with a binomial link function to ensure predictions ranged between zero and one (Elith & Leathwick, 2007). We then calculated dispersal cost surfaces for each species, where the cost of moving across a grid cell (at 1-km resolution) was inversely proportional to inferred climatic suitability. For each presence or pseudo-absence, we calculated the cost of the least cost pathway to 5000 randomly chosen cells (Fig. S2) on *Hispaniola* and summed these values to get an overall estimate of the difficulty of reaching a location; we call this method Cost1. Results using the sum of cost pathways to all cells were almost identical, so the latter was chosen to minimize computational time in the null model analysis (see below). We also computed an alternative measure of dispersal cost (Cost2), which incorporated spatial information on known occurrences of a species. For this method, we summed the least-cost pathways to known occurrences. We log-transformed both Cost1 and Cost2 because their distributions were extremely right skewed.

Fitting MARS distribution models

We fitted MARS models to data for the 26 Hispaniolan *Anolis* species (Table S2) that had at least 10 unique occurrence points. MARS models fit a series of piecewise basis functions to the data, using a stepwise procedure to add and remove basis functions until predictive performance (assessed using cross-validation) is maximized (Friedman, 1991; Leathwick *et al.*, 2005, 2006). We used MARS rather than other methods, like Maxent, that use random pseudo-absences (rather than target group pseudo-absences) because they could not incorporate morphological landscapes, as they would require information on the morphological composition of unsampled localities.

Full MARS models were fitted using the same parameters and procedure as described above. The set of predictor variables included six climatic principal components, two morphological landscapes and one of the dispersal cost landscapes. For each species, we recorded the shape of the basis functions (increasing, decreasing or complex; Fig. 1) to determine whether high values of MorphSim, MorphNbr and/or dispersal cost led to reduced suitability, as predicted. We evaluated model fit using explained deviance (D^2 ; Guisan & Zimmermann, 2000) and performed 10-fold cross validation to calculate the pooled (across all 10 subsamples) value of the area under the curve (AUC) of the receiver operating characteristic. Lastly, we calculated the independent contribution of morphological landscapes by dropping the relevant variables from the final generalized linear model and calculating the change in D^2 (Leathwick *et al.*, 2005). We performed a similar operation for dispersal cost. However, our measure of dispersal cost is based on climatic suitability and thus incorporates climatic effects, which may inflate its relative importance. To account for this, when we dropped Cost1 or Cost2, we added the climate basis functions from the climate-only model to estimate the contribution of dispersal cost independently of climate suitability. We implemented MARS models using the code provided by Elith & Leathwick (2007), which we modified as necessary to the specifics of our study.

We also fitted an additional set of models to determine whether our results were robust to the inclusion of phylogenetic similarity. These models were fitted as above, but with PhySim and PhyNbr added to the set of predictor variables.

Null species distributions

We compared our MARS results with those based on sets of null species occurrences that had the same spatial structure as observed species occurrences but were generated without consideration of climate, morphology, phylogeny or dispersal barriers (Fig. S3). For each species in our analysis, we calculated the pair-wise distances (PDs) among its occurrences. We then fitted a variety of distributions (normal, log-normal, exponential, and Weibull) to the distribution of PDs and selected the one with the maximum likelihood value. Next, we chose a random locality on *Hispaniola* as a species' initial occurrence. A second occurrence was then placed using a random direction and a distance drawn from the fitted PD distribution. This was repeated until the number of null occurrences equalled the observed number for a species. Next, following Beale *et al.* (2008), we used an iteration procedure to maximize the similarity between observed and null spatial structure. First, we calculated the Kolmogorov–Smirnov statistic (KS-D) as a measure of concordance among the null and observed distributions of PDs. Next, we randomly deleted an occurrence and replaced it using the above procedure. This process was repeated until KS-D reached a pre-determined threshold. We chose a threshold of 0.281, which corresponds to a P -value of 0.05 for the median number of occurrence points in our data (22). For small sample sizes, we relaxed this threshold because it was almost impossible to achieve (thresholds for small sample sizes, n , were: $n < 4$, $KS-D_{\text{Threshold}} = 0.7$; $n = 4$, $KS-D_{\text{Threshold}} = 0.5$; $5 < n < 10$, $KS-D_{\text{Threshold}} = 0.4$). We generated 100 sets of null occurrences, where each set included null occurrences for each species. R code to generate null occurrences is available from A.C.A.

For each set of null occurrences, we performed our entire MARS analysis. This involved merging occurrences <3000 m apart, calculating morphological, phylogenetic and dispersal cost landscapes and fitting MARS models. This procedure resulted in slight variation in the number of occurrences for each species and the number of target-group pseudo-absences, because null co-occurrence was generally less than observed co-occurrence. We compared the results of null analyses with the observed results to determine whether the latter were likely, even if the spatial structure of species' occurrences arose entirely from processes unrelated to climate, dispersal barriers, phylogeny, or niche incumbency.

RESULTS

Morphological landscapes (Figs 2 & S4) were selected for inclusion in the full MARS model by the adaptive fitting process for 13 of 26 species when Cost1 was used and 10 species when models included Cost2 (Tables S2 & S3). The 10 species set for Cost2 models was a subset of the Cost1 set and included: *Anolis baho-*

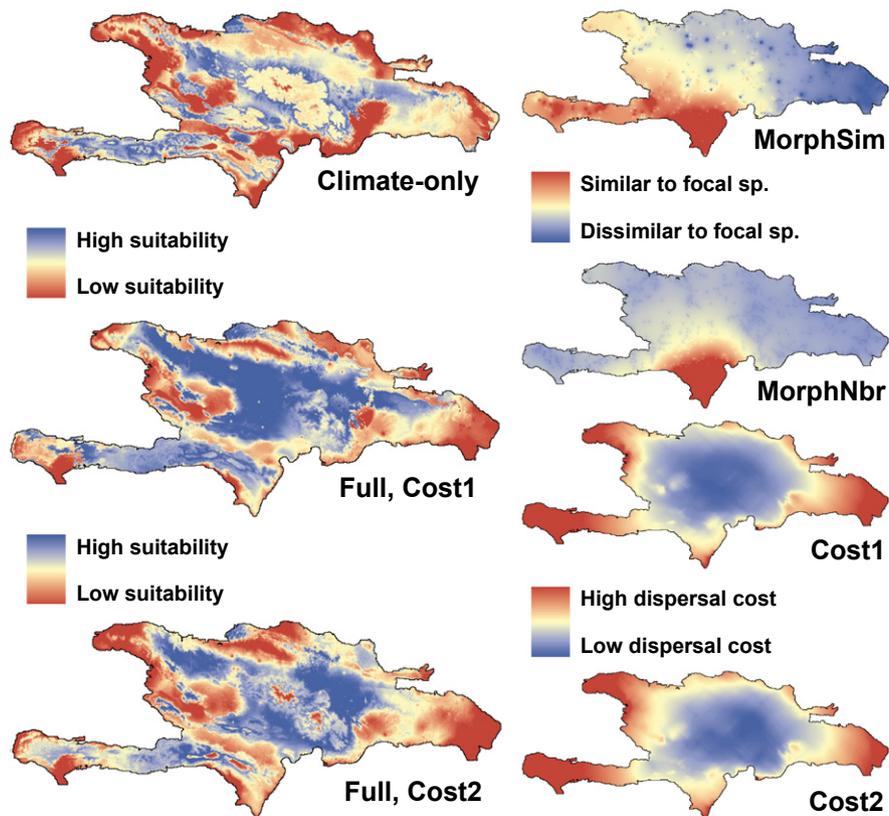


Figure 2 An example of a species' distribution (*Anolis semilineatus*) modelled using only climate variables and the full set of variables, along with the underlying morphological and dispersal cost landscapes. For modelled distributions (left column and legends), suitability values are relative and are not equal to probability of occurrence (though we expect them to be correlated) which cannot be modelled without independent data on species prevalence across Hispaniola (Elith *et al.*, 2011). Full models were fitted including climate, morphological landscapes and either Cost1 or Cost2 dispersal cost surfaces. For morphological and dispersal cost landscapes (right column and legends), 'favourable' conditions are those with low morphological similarity to the focal species (*A. semilineatus*) and low costs of dispersal. MorphSim is the maximum morphological similarity to the focal species of those species present at a locale, MorphNbr is the distribution of the focal species' nearest neighbour in morphological space (*A. alumina* in this case). For display purposes, MorphSim and MorphNbr surfaces were interpolated from occurrence points using inverse distance weighting. Cost1 estimates dispersal cost from randomly chosen points, while Cost2 estimates dispersal cost from known occurrences of the focal species.

rucoensis, *Anolis brevirostris*, *Anolis chlorocyanus*, *Anolis christophei*, *Anolis cybotes*, *Anolis distichus*, *Anolis monticola*, *Anolis semilineatus*, *Anolis shrevei* and *Anolis websteri* (Tables S2 & S3). Morphological landscapes for *Anolis ricardii*, *Anolis coelestinus* and *Anolis singularis* were selected only when Cost1 was used. Many of these species are parapatrically distributed with species in the same ecomorph, for example: *A. chlorocyanus* with *A. coelestinus*, *A. ricardii* with *A. baleatus* (morphology was not included in the full MARS model for *A. baleatus*) and *A. semilineatus* with *A. bahorucoensis*. Consistent with our prediction, we found that the vast majority of morphological basis functions had a decreasing shape, i.e. low estimated suitability when similarity to incumbent species was high (Fig. 3). Only the model for *A. monticola* did not include a decreasing morphological landscape function (Tables S2 & S3). The number of decreasing morphological basis functions was much greater than expected based on sets of spatially structured null species occurrences, regardless of which cost surface was used ($P < 0.01$ for both).

Dispersal cost surfaces (Figs 2 & S4) were included in the final models for most species, especially when Cost2 was utilized (Cost1, 19 species; Cost2, 25 species). Only *A. bahorucoensis* was not included in either set (Tables S2 & S3). As predicted, the vast majority of basis functions were decreasing (Fig. 3). However, when Cost1 was considered, the number of decreasing basis functions did not differ from the null expectation, based on simulated species occurrences ($P = 0.16$); this result was close to significant when Cost2 was used ($P = 0.08$).

Overall, the incorporation of morphology and dispersal cost into models resulted in smaller predicted distributions than climate-only models (Figs 2 & S4). We found that the mean AUC and D^2 (proportion of explained deviance) of our full models were significantly greater than expected based on species null occurrences ($P < 0.01$ for both Cost1 and Cost2; Fig. 4). However, there was substantial variation in AUC and D^2 across all species (Fig. 5; Tables S2 & S3). The average change in AUC between full and climate-only models was 0.02 (range -0.09 to

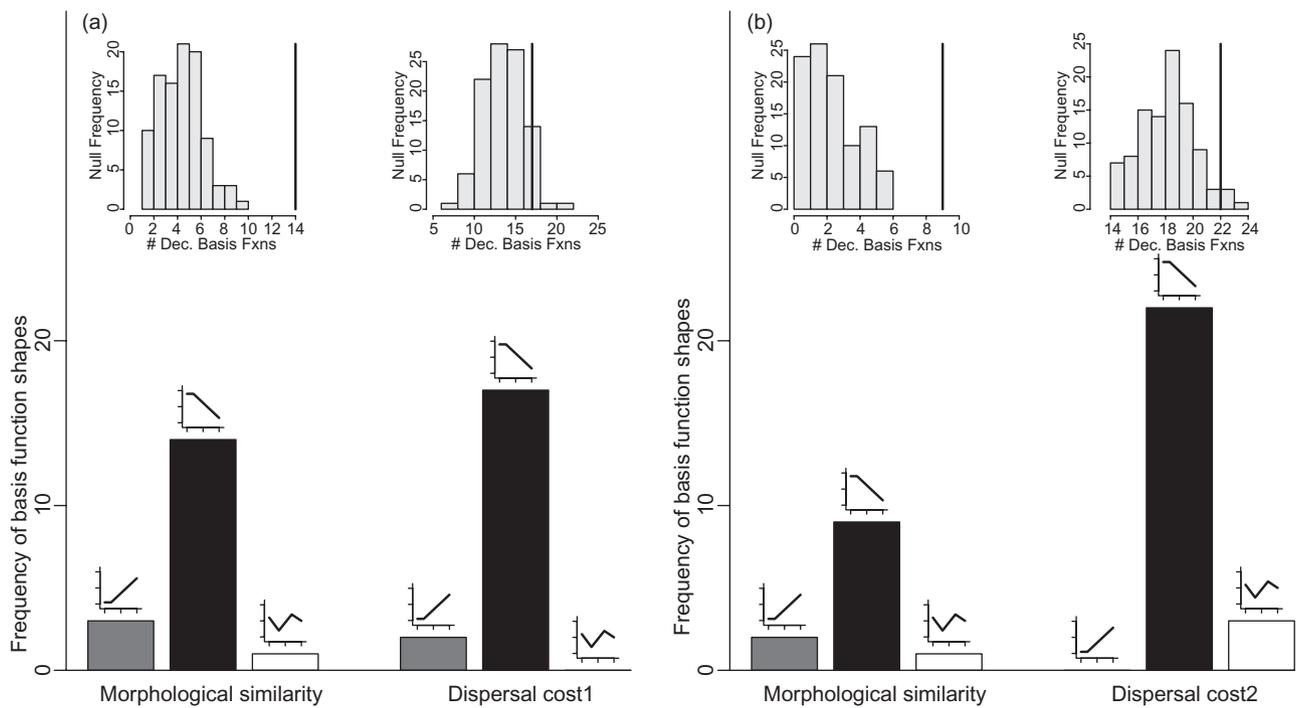


Figure 3 The frequency of basis function shapes from multivariate adaptive regression spline (MARS) models that included climate, dispersal cost and morphological similarity as predictors across 26 *Anolis* species. (a) Models fitted with Cost1, which estimated dispersal cost from randomly chosen locations. (b) Models fitted with Cost2, which estimated dispersal cost from known occurrences of the focal species. Small insets depict example basis function shapes. Decreasing basis functions (black bars) are predicted if niche incumbency and environmental barriers limit species ranges, while increasing (dark grey) and complex (white) functions are not. Inset histograms depict the number of decreasing basis functions for morphological and dispersal cost obtained from 100 null simulations; vertical lines depict the observed number, demonstrating that decreasing basis functions were more common than expected by chance for morphological similarity ($P < 0.01$) but not for dispersal cost ($P > 0.07$).

0.12) for Cost1 and 0.06 (range -0.10 to 0.14) for Cost2. Similarly, D^2 increased by an average of 0.027 (range -0.25 to 0.10) for Cost1 models and 0.11 for Cost2 (range -0.02 to 0.32 ; Fig. 5). Negative changes in D^2 can occur as a result of the adaptive model fitting process.

On average, decreasing morphological landscapes made relatively small unique contributions to total D^2 (Fig. 6). Despite its small magnitude, the probability of observing an average unique contribution of decreasing morphological landscapes across all species as large as we did was unlikely to have occurred by chance and was consistent across Cost1 and Cost2 models ($P < 0.05$ for both). The unique contribution of dispersal cost when estimated using Cost1 was similar to that of morphology, but increased under Cost2, which incorporated information on where species were known to occur. However, the observed contribution of dispersal cost was not greater than expected based on null species occurrences, regardless of which cost surface was used ($P > 0.30$ for both).

All of these results were broadly robust to including phylogenetic similarity landscapes. The set of species whose models included decreasing MorphSim or MorphNbr functions changed only slightly when phylogeny was considered (compare Tables S2 & S3 with Tables S4 & S5). However, the major results were identical: decreasing morphological landscape functions were more common ($P < 0.01$) and explained more deviance (P

< 0.03) than expected based on our null model (Figs S5 & S6), while the number of, and deviance explained by, decreasing dispersal cost functions was not greater than the null expectation ($P > 0.13$ for all tests except for the number of decreasing Cost2 functions which had $P = 0.07$; Table S5). Relative to the null model, we found no preponderance of decreasing phylogenetic landscape functions (Figs S5 & S6; $P > 0.16$), nor did they explain more deviance than expected by chance ($P > 0.32$). PhyNbr, which represents the distribution of each species' closest relative, was included for only a single species each in Cost1 and Cost2 models (Tables S3 & S4).

DISCUSSION

Niche incumbency

Although theory suggests that biotic interactions can limit species distributions, whether they do or not has long been controversial (Hutchinson, 1957; Diamond, 1975; Connor & Simberloff, 1979; Case *et al.*, 2005; Soberón, 2007; Holt, 2009; Simberloff & Collins, 2010). Here, we found empirical evidence consistent with ecological niche incumbency limiting species distributions. For more than a third of the 26 species examined, regions where a morphologically similar species occurred had

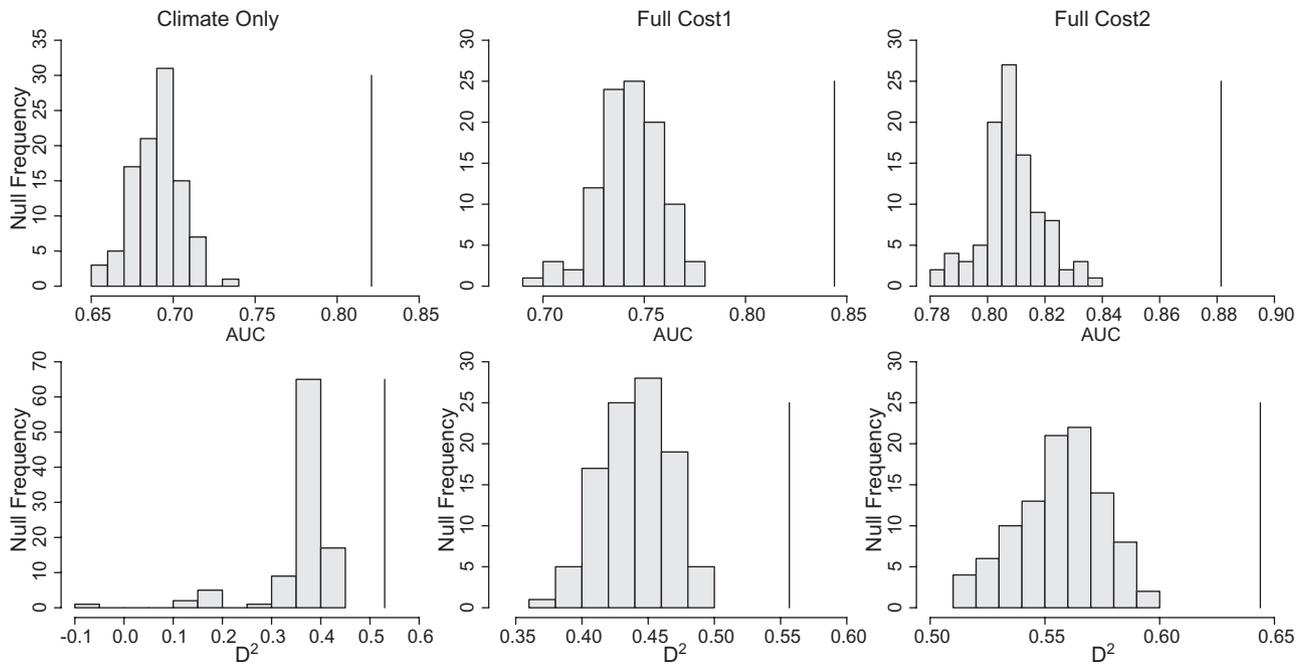


Figure 4 The mean area under the curve (AUC) and D^2 across 26 species (vertical line) compared with the distribution of mean AUC and D^2 values (histograms) from our null model analysis. Results from climate-only and full (climate, morphological similarity and dispersal cost) models fitted to real and null species occurrence data are shown. Full models included climate variables, morphological landscapes with and either Cost1 (estimated dispersal cost from randomly chosen locations) or Cost2 (estimated dispersal cost from known occurrences of the focal species). Observed mean AUC and D^2 values differed significantly from the null expectation ($P < 0.01$).

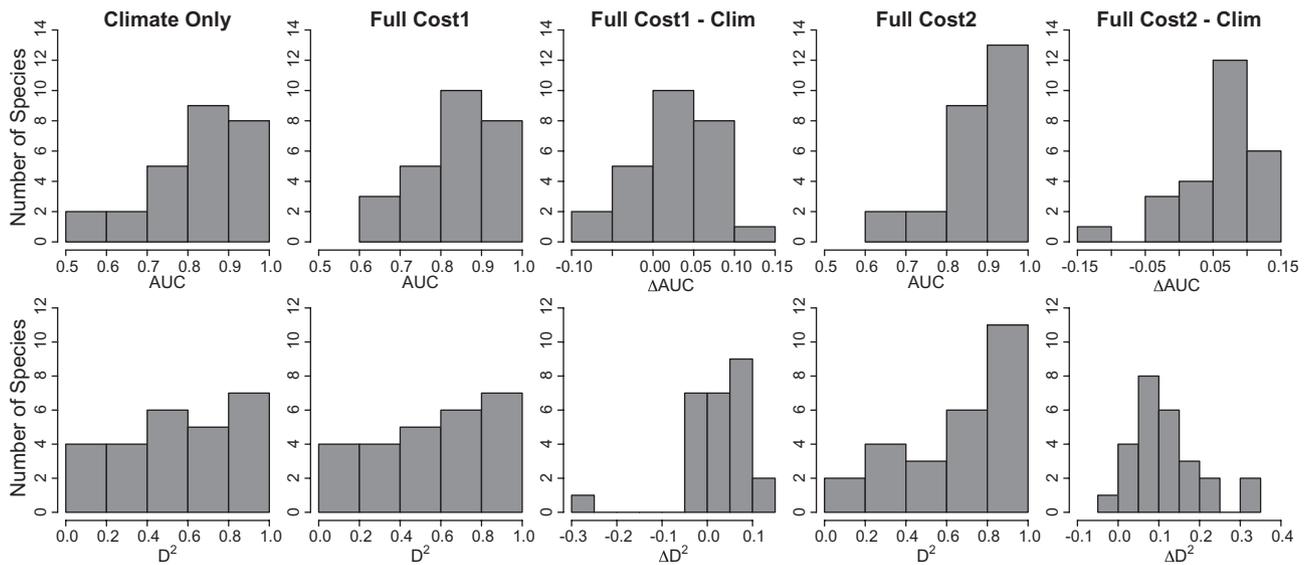


Figure 5 Variation and improvement in model fit and accuracy across climate only and full models for all 26 *Anolis* species. Full models included climate variables, morphological landscapes and either Cost1 (estimated dispersal cost from randomly chosen locations) or Cost2 (estimated dispersal cost from known occurrences of the focal species). AUC is the area under the curve of the receiver operating characteristic, estimated using 10-fold cross validation and D^2 is explained deviance. ΔAUC and ΔD^2 represent the difference between the relevant full model and climate-only models.

lower modelled suitability, even when those areas were climatically suitable and available for colonization. These findings were robust to alternative methods of dispersal cost estimation and were distinguishable from a null model that maintained the

spatial structure in species occurrences, suggesting that inter-specific interactions can be sufficiently strong and consistent through time to leave a signal in broad-scale biogeographical patterns.

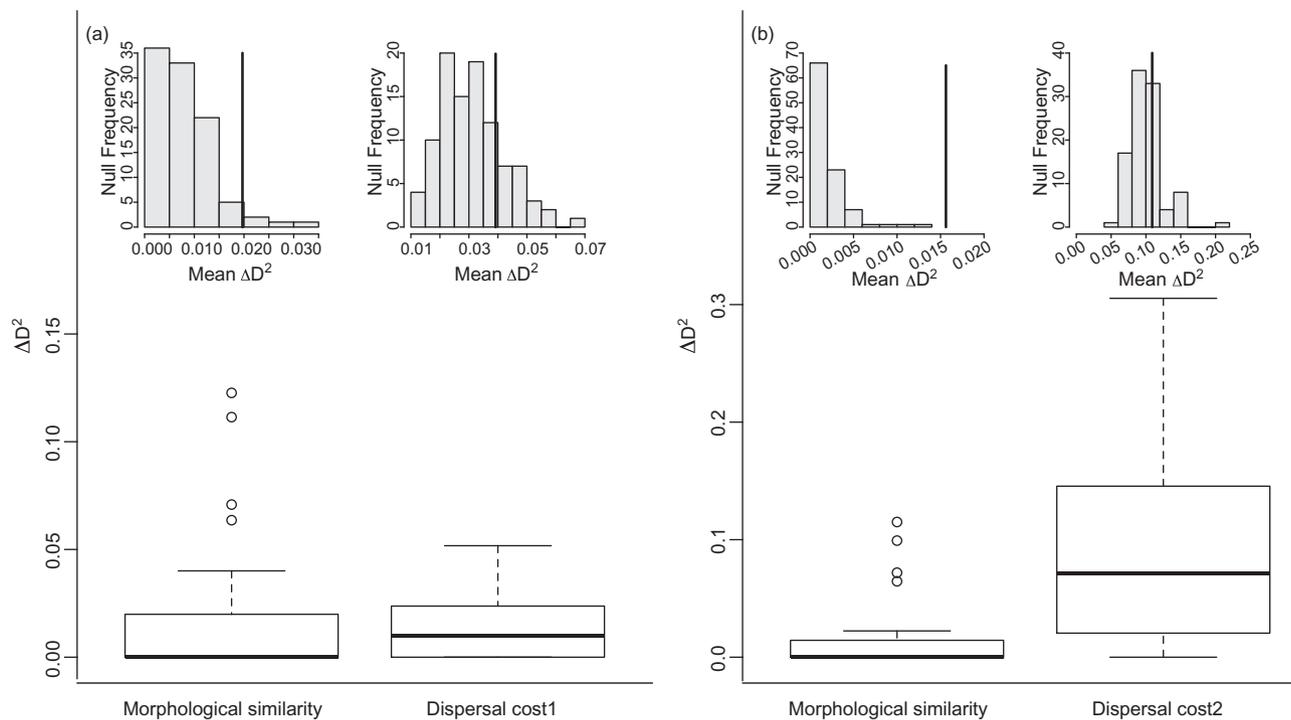


Figure 6 The unique contribution of decreasing morphological and dispersal cost landscape basis functions to full models. Full models included climate variables and morphological landscapes with either Cost1 (estimated dispersal cost from randomly chosen locations) or Cost2 (estimate dispersal cost from known occurrences of the focal species). (a) Results when models were fitted with Cost1. (b) Results when models were fitted with Cost2. ΔD^2 is the absolute value of the change in D^2 when corresponding basis functions were dropped from the final generalized linear model. Inset histograms show the null distribution of mean ΔD^2 values from our null simulations along with the mean from the real data (vertical line). Observed ΔD^2 was significantly greater for morphological similarity in both cases ($P < 0.05$), but not for dispersal cost ($P > 0.30$).

The lack of co-occurrence of morphologically similar species at broad scales was not a by-product of the geography of speciation. Species that have undergone allopatric speciation may not overlap geographically if speciation has happened too recently for ranges to expand (Barraclough & Vogler, 2000). As many closely related anoles are morphologically similar, insufficient time after allopatric speciation could produce a pattern of low co-occurrence of morphologically similar species that is not due to niche incumbency, provided range dynamics are sufficiently slow (Losos & Glor, 2003). This was not the case for Hispaniolan anoles. If it were, then the distribution of a species' closest relative (our PhyNbr landscape) should be a better predictor of a species' distribution than morphological similarity. However, the PhyNbr landscape was rarely selected for inclusion in our models (once for each cost surface) and considering it did not reduce the signal of morphological similarity on species distributions. Thus, although many morphologically similar anoles are close relatives, our analysis suggests that the signal we detected is due to niche incumbency and is not confounded by insufficient time post-allopatric speciation.

Since the debates on community assembly rules of the 1970s and 1980s (e.g. Diamond, 1975; Connor & Simberloff, 1979), ecologists have recognized that negative co-occurrence alone is insufficient evidence for niche incumbency. This is because species may not co-occur simply by chance and/or because dis-

persal limitation and habitat differences among species can also produce checkerboard patterns (Belmaker & Cooper, 2010; Simberloff & Collins, 2010). The judicious use of null models can partially ameliorate the confounding effects of dispersal limitation and chance (e.g. Gotelli *et al.*, 2010), but they cannot exclude all alternative explanations (Belmaker & Cooper, 2010; Simberloff & Collins, 2010). Here, because the traits we examined were correlated with both macrohabitat (e.g. xeric versus mesic; Glor *et al.*, 2003) and microhabitat use (e.g. grass–bush versus trunk–crown; Losos, 2009), it is unlikely that the lack of co-occurrence among morphologically similar species arose from different habitat requirements. Nor is it likely to have occurred by chance as more species had negative morphological landscape basis functions (and their effects were stronger) than predicted by our null model of species occurrences.

Past niche-modelling studies of how species interactions affect geographical distributions have been limited to pairs (or trios) of species (e.g. Anderson *et al.*, 2002; Buckley & Roughgarden, 2006; Pellissier *et al.*, 2010; Rubidge *et al.*, 2011). In contrast, Hispaniolan anoles are an exceptionally diverse group (Losos, 2009; Algar & Losos, 2011). The importance of considering a diverse potential set of interactions is highlighted by the relative frequency of the MorphSim and MorphNbr landscapes in our fitted models. The MorphSim variable quantified the maximum morphological similarity across all species at a

locality, while MorphNbr considered only the occurrence of the nearest neighbour in a morphological space that included nearly all Hispaniolan anoles. The MARS algorithm selected MorphSim more often, suggesting that a species' distribution may be limited by interactions with similar phenotypes, but different species, across its range.

Although we considered a diverse set of potentially interacting species, our findings are probably still conservative with respect to niche incumbency. This is because we only considered congeneric interactions. Other taxa may have similar niches to anoles, especially insectivorous birds and frogs, and could further limit anole distributions. However, we expect anole–anole interactions to be strongest: lower diet overlap between anoles and birds than between anoles (Wright, 1981; Adolph & Roughgarden, 1983) and activity time differences between anoles and frogs may limit the potential for niche incumbency (Reagan *et al.*, 1996; Losos, 2009). Nonetheless, such interactions could contribute to niche incumbency-based limits to anole distributions beyond those detected here.

The ecological relevance of the selected traits

A critical consideration for trait-based ecological studies is the ecological relevance of selected traits. Three lines of evidence suggest that morphological similarity is a suitable proxy for the likelihood of niche incumbency among anoles.

1. Inter-specific variation in the morphological traits we examined produces variation in functional capabilities that are correlated with differences in habitat use and behaviour (Irschick & Losos, 1998, 1999; reviewed in Losos, 2009).
2. Body size differences among sympatric species are linked to differences in prey use (Rand & Williams, 1969; Schoener, 1970; Losos, 2009).
3. Experimental manipulations have demonstrated that degree of competitive interaction is related to morphological similarity (e.g. Pacala & Roughgarden, 1985). Additionally, introductions of anoles are less likely to be successful if there is an ecologically, and usually morphologically, similar species already present (Losos *et al.*, 1993).

Alternatives to niche incumbency

Not all species displayed patterns consistent with niche incumbency. This could be due to divergence along a niche axis upon which morphological adaptation in the measured traits has not occurred. Consistent with this explanation, some anoles are known to partition thermal microhabitats (sun versus shade), which can allow for sympatry of otherwise ecologically similar species (Rand & Williams, 1969; Losos *et al.*, 2003; Rodríguez-Schettino *et al.*, 2010). Our selected morphological traits were not related to thermal habitat partitioning and thus could not quantify differentiation along this niche axis.

The lack of patterns consistent with niche incumbency in some species does not necessarily imply unmeasured niche divergence. Instead, climate and/or dispersal limitation alone could limit these species distributions, or; congeneric interac-

tions may have been insufficiently strong to leave a signal at broad scales. Other factors, such as geographical intraspecific variation, could also have masked the effects (Schoener, 1970). Lastly, other biotic interactions, such as predation, which can reduce anole abundance (Schoener *et al.*, 2002), or parasitism, could also limit distributions. However, our knowledge of the prevalence or importance of such interactions is currently very limited, especially for the latter (Losos, 2009).

Alternatively, incomplete reproductive isolation among close relatives could also prevent co-occurrence of morphologically similar species, if colonizers of one species are assimilated by the incumbent species (Losos, 1990; Cavender-Bares *et al.*, 2009). Under such a process, we would predict decreasing phylogenetic similarity basis functions to be more prevalent than increasing ones, and more common in models than morphological similarity. Neither of these were the case. However, in the absence of estimates of reproduction isolation and hybridization, we cannot exclude this explanation entirely.

Dispersal limitation

Our results suggest that dispersal limitation also contributed to distributional limits, though the underlying processes remain difficult to distinguish. We cannot confidently differentiate between a role for environmental barriers and processes that lead to climate-independent spatial clustering of species occurrences. However, the prevalence of decreasing dispersal cost basis functions suggests that environmental barriers prevent some species from reaching climatically suitable areas. This conclusion matches Glor & Warren's (2011), who found that unsuitable habitat maintained the boundary between *A. coelestinus* and *A. chlorocyanus* in southern Hispaniola. Accordingly, dispersal cost was included in our models for both of these species; morphology was also included (except for the Cost2 model for *A. coelestinus*), which is consistent with Glor & Warren's (2011) suggestion that niche incumbency supplements primary limitations imposed by environmental barriers.

Despite concordance in the specific case of *A. chlorocyanus* and *A. coelestinus*, across all species our results for dispersal barriers did not differ from the null expectation in numbers (though it was close to significance for Cost2 models) nor in the unique contribution to D^2 . Thus, inherent spatial clustering (which must arise because of some type of dispersal limitation) rather than environmental barriers could underlie a portion of this effect. Incorporating distance from known occurrences (Cost2) increased the relative importance of dispersal-cost surfaces. Even with this increase in D^2 there was little difference from the null expectation, which is hardly surprising as the possible distances from a species' occurrences are, to a large extent, a function of their spatial clustering. However, our null model analysis was extremely conservative. It assumed that none of the clustering in species occurrences arose from the spatial structure of the abiotic environment, which is unlikely to be the case (Peterson *et al.*, 2009). Thus, it almost certainly overestimated the importance of non-climate-related dispersal limitation.

The importance of climate

Detectable effects of niche incumbency and dispersal limitation on some species distributions does not imply that climatic variables are unimportant. Rather, they accounted for most of the deviance explained by our full models. Trait and dispersal cost landscapes contributed relatively small additional amounts to the overall model fit and accuracy, suggesting that niche incumbency and dispersal barriers (which also include an indirect climatic effect) only supplement climate in limiting the distributions of these island lizards. However, our results are likely to be conservative with respect to niche incumbency and dispersal barriers because we quantified realized, rather than fundamental, climatic niches (Kearney & Porter, 2004). Our estimates of climatic suitability were based on the conditions in which a species has been observed and may exclude areas on the edge of the fundamental niche where it is absent due to niche incumbency or dispersal limitation. Such scenarios may even be likely given that a species' competitive ability is likely to decline toward its fundamental niche edge. The prevalence of parapatrically distributed species in our niche incumbency set is consistent with this explanation. Thus, our estimates should be viewed as a conservative estimate of the contributions of niche incumbency to distributional limits. However, the strength of climate relationships is so strong that even had we been able to measure fundamental niches, it is likely that climate would remain a major contributing factor shaping the distributions of Hispaniolan anoles.

CONCLUSION

We used species traits and estimates of dispersal cost to incorporate multiple dimensions of the ecological niche into traditional climate-based distribution models. By simultaneously including factors relating to climatic limits, dispersal limitation and niche incumbency, we have shown that niche incumbency and dispersal constraints complement, rather than preclude, climatic limits to species distributions. However, the relative importance of these processes varied markedly among species. A critical question for the future will be to determine the source of this variation, e.g. why niche incumbency was detectable for some species but not others, and, ultimately, whether these differences are predictable. More generally, coupling of trait-based approaches with the empirical strength of species distribution modelling has considerable potential to provide new insights into how complementary processes interact to produce and maintain general biogeographical patterns.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Figure S1 The total set of localities across all 37 species.

Figure S2 Five thousand randomly selected localities for calculating Cost1.

Figure S3 Observed and null species occurrences.

Figure S4 Modelled distributions and morphological, phylogenetic and cost landscapes.

Figure S5 Frequency of basis function shapes in full models including phylogeny.

Figure S6 Unique contribution of decreasing basis functions to models including phylogeny.

Table S1 Principal component analysis on climate variables.

Table S2 Summary of multivariate adaptive regression spline outputs for Climate-only and Cost1 full models.

Table S3 Summary of multivariate adaptive regression spline outputs for Cost2 full models.

Table S4 Summary of multivariate adaptive regression spline outputs for Cost1 full models including phylogeny.

Table S5 Summary of multivariate adaptive regression spline outputs for Cost2 full models including phylogeny.

BIOSKETCH

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A.C.A. and J.B.L. conceived and designed the research. D.L.M. and R.E.G. collected and contributed data. A.C.A. performed the analyses and wrote the manuscript with contributions from J.B.L., D.L.M. and R.E.G.

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