



Area, climate heterogeneity, and the response of climate niches to ecological opportunity in island radiations of *Anolis* lizards

Adam C. Algar^{1*} and D. Luke Mahler²

¹School of Geography, University of Nottingham, Sir Clive Granger Building, Nottingham NG7 2RD, UK, ²Biodiversity Institute, The University of Kansas, Lawrence, KS 66044, USA

ABSTRACT

Aim Rates of climate niche evolution underlie numerous fundamental ecological processes and patterns. However, while climate niche conservatism varies markedly among regions and clades, the source of this variation remains poorly understood. We tested whether ecological opportunity can stimulate radiation within climate niche space at biogeographic scales, predicting that rates of climate niche evolution will scale with geographic area and climate heterogeneity.

Location Caribbean

Methods We quantified two temperature axes (mean temperature and temperature seasonality of species' localities) of the climate niche for 130 *Anolis* species on Cuba, Hispaniola, Puerto Rico, Jamaica and the northern and southern Lesser Antilles. Using a species-level phylogeny, we fitted macroevolutionary models that either constrained rates of climate niche evolution or allowed them to vary among regions. Next, we regressed region-specific evolutionary rates against area, species richness and climate heterogeneity. We evaluated whether results were robust to uncertainty in phylogenetic and biogeographic reconstructions and the assumed mode of evolution.

Results For both niche axes, an Ornstein-Uhlenbeck model that allowed the net rate of evolution (σ^2) to vary among island groups fit the data considerably better than a single-rate Brownian motion model. Nagelkerke pseudo- R^2 values of the fit of these OU models to mean temperature and seasonality axes were 0.43 and 0.66, respectively. Evolutionary rates for both axes were higher in larger areas, which also have more species. Only the rate of mean occupied temperature evolution was positively related to climate heterogeneity, and only after accounting for region size.

Conclusions Rates of climate niche evolution scale consistently with the area available for radiation, but responses to climate heterogeneity vary among niche axes. For the mean temperature axis, climate heterogeneity generated additional opportunities for radiation, but for seasonality it did not. Overall, the physical setting in which a clade diversifies can influence where it falls on the evolutionary continuum, from climate niche conservatism to radiation.

Keywords

Adaptive radiation, *Anolis*, climate heterogeneity, climate niche, ecological opportunity, evolutionary rates, island biogeography, niche conservatism, niche evolution.

*Correspondence: Adam C. Algar, School of Geography, University of Nottingham, Sir Clive Granger Building, Nottingham NG7 2RD UK. E-mail: adam.algar@nottingham.ac.uk

INTRODUCTION

The implications of climate niche conservatism for myriad ecological patterns and processes are now well recognized (e.g. Wiens *et al.*, 2010). However, rates of climate niche evolution vary markedly among clades and regions (Evans *et al.*, 2009; Kozak & Wiens, 2010; Cooper *et al.*, 2011; Fisher-Reid *et al.*, 2012; Schnitzler *et al.*, 2012; Lawson & Weir, 2014), and there have been comparatively few efforts to determine why some clades diversify in climate space while others do not. Several recent studies have suggested that organismal features, such as life-history, growth form, or resource specialization may constrain climate niche evolution as lineages radiate (Smith & Beaulieu, 2009; Cooper *et al.*, 2011). Here, we examine the potential for extrinsic factors to explain variation in climate niche diversification (Cooper *et al.*, 2011; Lawson & Weir, 2014), and we test whether rates of climate niche evolution depend on available geographic area and climate heterogeneity within a region. In doing so, we test whether the ecological opportunity hypothesis, which explains evolutionary radiation along other niche axes (Schluter, 2000), can also predict rates of climate niche evolution at biogeographic scales.

Ecological opportunity, the existence of under utilized resources, or unoccupied niche space, is thought to drive adaptive radiation (Simpson, 1953; Schluter, 2000; Glor, 2010; Losos, 2010; Losos & Mahler, 2010; Yoder *et al.*, 2010). Ecological opportunity can be generated in many ways, including the evolution of a trait allowing individuals to interact with the environment in a new way ('key innovation'), mass extinction, or colonization of biotically depauperate areas (Schluter, 2000; Losos & Mahler, 2010). Though it often takes the form of food resources, ecological opportunity can also be manifest as spatial environmental heterogeneity. For example, *Anolis* lizards have repeatedly radiated to use a variety of structural microhabitats in the Greater Antilles (Mahler *et al.*, 2010), while African cichlids and Pacific rockfish (*Sebastes*) have diversified along depth gradients (Seehausen, 2006; Ingram, 2011).

In this paper, we describe 'climate opportunity' as a range of novel climatic environments that are physically accessible to a potentially radiating lineage; we view it as one type of ecological opportunity. Climate opportunity should scale with the diversity of climate conditions available in a region. At one extreme, when climate is uniform through space, each species' realized climate niche [i.e. the climate conditions in which it occurs (Cooper *et al.*, 2011; Fisher-Reid *et al.*, 2012; Schnitzler *et al.*, 2012)] will be identical and the rate of climate niche divergence among species is constrained to be zero. However, as climate heterogeneity increases, niche shifts can occur, climate specialists can evolve, and the rate of climate niche evolution can increase. Thus, we predict a positive relationship between the rate of climate niche divergence within a clade, and the climate heterogeneity of a region.

Many clades fail to radiate ecologically in the presence of apparent opportunities (Seehausen, 2006; Losos, 2010; Losos & Mahler, 2010). Here, we hypothesize that the geographical area available for radiation helps determine whether lineages success-

fully exploit climate opportunity. Small areas may limit climate niche radiation for several reasons. Cladogenetic speciation requires sufficient area in most organisms, and species diversification rate is known to scale with area in adaptive radiations (Losos & Schluter, 2000; Wagner *et al.*, 2014). In small but still heterogeneous regions, climate specialization and divergence may be limited by gene flow between dissimilar, but spatially proximate, environments (Doebeli & Dieckmann, 2003). Also, if climate specialists do arise in small regions, they will have restricted ranges and/or small population sizes. They therefore may face higher extinction rates than species with larger ranges (Gaston, 1998; Ricklefs & Bermingham, 2008; Cornell, 2013). Area may also affect climate niche evolution indirectly; for example, large areas have more species, which may increase competitive interactions leading to niche divergence. In summary, clades should be more able to take advantage of climate opportunity in large areas where geographic isolation permits speciation (and persistence), coupled with local adaptation and niche divergence (Seehausen, 2006; Kisel & Barraclough, 2010). Thus, we predict that rates of climate niche evolution should be lowest in small, climatically uniform regions and highest in large, climatically diverse ones. We test these predictions using Caribbean *Anolis* lizards.

MATERIALS AND METHODS

Study system

We tested whether climate opportunity drives climate niche radiation for *Anolis* lizards on the Greater and Lesser Antilles. These islands vary markedly in both size and climate heterogeneity (Fig. 1). Due to a lack of within-island speciation on individual Lesser Antillean islands (Losos & Schluter, 2000), we treated the northern and southern Lesser Antilles as single conglomerates (Fig. 1) when calculating total land area, climate heterogeneity, and evolutionary rates, as they are each inhabited by a single *Anolis* clade (Fig. S1). We address how the fragmented nature of the northern and southern Lesser Antilles may have influenced rates of climate niche evolution in the Discussion. Our approach yielded six regions: Cuba, Hispaniola, Puerto Rico, Jamaica, the northern Lesser Antilles, and the southern Lesser Antilles. To summarize temperature heterogeneity, we first performed a principal component analysis on the eleven Worldclim (Hijmans *et al.*, 2005) temperature variables at 30 arcsec resolution across the entire study area. Next, we summarized two axes of temperature heterogeneity for each of our six regions by computing the standard deviation of all scores (at 30 arcsec resolution) for the first and second principal components (PC1 and PC2) in each region. PC1 explained nearly 60% of the total variance and was correlated most strongly with mean annual temperature and temperature extremes (Table S1 in Supporting Information). PC2 explained 25% of the total variance and correlated most strongly with annual temperature seasonality (standard deviation of monthly means) and annual temperature range (Table S1).

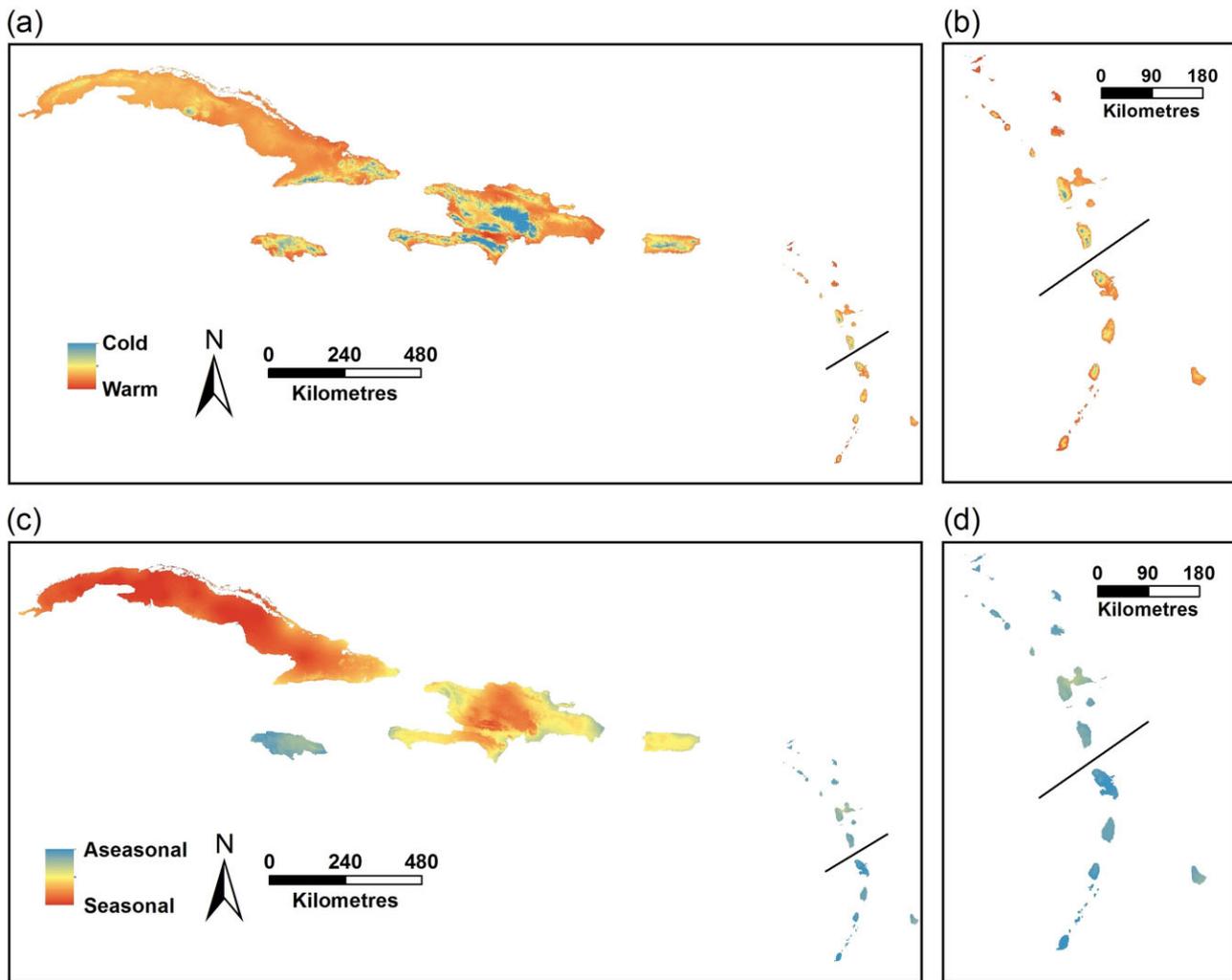


Figure 1 Temperature variation on the Greater and Lesser Antilles. (a) and (c) show all islands and (b) and (d) magnified views of the Lesser Antilles. (a) and (b) are the first principal component scores of a PCA on the Worldclim temperature variables, used to measure temperature niche position (Table S1). (c) and (d) are the scores from PC2, used to measure the temperature seasonality niche axis. The black line shows the boundary between the northern and southern Lesser Antilles.

Quantifying the climate niche

Species occurrences were taken either from natural history museum collection records (accessed via HerpNet; (<http://www.herpnet.org>) or published sources (Schwartz & Henderson, 1991; Algar & Losos, 2011; Algar *et al.*, 2013). Our final data set for 139 species (130 island and 9 mainland) was composed of 5534 occurrences (Appendix S1) at 3399 unique localities (median occurrences per species = 13). We used the means of PC1 and PC2 at species' occurrence localities as two complementary measures of the temperature axis of the climate niche (Cooper *et al.*, 2011; Fisher-Reid *et al.*, 2012; Schnitzler *et al.*, 2012). The mean of PC1 was highly correlated with other measures such as minimum (Pearson's $r = 0.75$, $P < 0.001$) and maximum (Pearson's $r = 0.78$, $P < 0.001$) temperatures of occurrence, based on Worldclim data, and represents a species' niche position with respect to temperature. Alternatively, the

mean of PC2 is a measure of the temperature seasonality niche axis (Fisher-Reid *et al.*, 2012; Lawson & Weir, 2014).

Phylogeny

We used Mahler *et al.*'s (2010) relative time-calibrated anole phylogeny, which is almost complete at the species level for the Greater and Lesser Antilles (it contains 117 species from the regions for which we had locality data). We added 13 missing species to the tree using a modified version of the add.random function in phytools v0.2–40 (Revell, 2012). This function randomly adds species to a tree where the probability of a species being added to a branch is proportional to branch length. However, we constrained the potential phylogenetic positions of these species based on their known taxonomic affinities, restricting them to subclades containing between two and four species (Table S2). We accounted for uncertainty from the addition of

missing species by repeating our analyses using a set of 50 random-addition trees. Each tree in this set was composed of the Bayesian maximum clade credibility chronogram of Mahler *et al.* (2010) with species added randomly; we call this the MCC-set. To account for uncertainty in phylogenetic relationships and the timing of diversification, we randomly chose 50 trees from a larger sample of 898 trees from the Bayesian posterior distribution of chronograms (Mahler *et al.*, 2010). Missing species were then added following the procedure described above; we call this the sample-set of trees.

Fitting macroevolutionary models

We reconstructed the colonization history of *Anolis* by computing marginal ancestral state estimates in phytools using a symmetric model with equal transition rates (e.g. Fig. S1; Yang *et al.*, 1995; Revell, 2012) and assigning the most likely state (region) to each node and subtending branch. Because the southern Lesser Antillean clade likely colonized the Antilles from the mainland, we included nine mainland species from the sister clade in our reconstructions. We also tested whether our major findings were sensitive to uncertainty in the reconstruction of *Anolis* colonization history (Appendix S2). Next, using the maximum clade credibility tree, we compared support for the accelerating-decelerating (ACDC) model, as implemented by Harmon *et al.* (2010), to Ornstein-Uhlenbeck (OU) and Brownian motion (BM) models for the major clades in each region (Fig. S2). As there was no evidence of an exponential deceleration in rate ('early bursts', *sensu* Harmon *et al.*, 2010) in the ACDC models (Table S3), we next fit a set of flexible BM and OU models in which we either constrained parameters to be equal for all lineages or allowed them to vary by region (Beaulieu *et al.*, 2012). Reliable solutions to OU models with jointly varying σ^2 and α parameters (OUMVA) could not be obtained and these models were omitted. Again, the nine mainland species were included in model fitting. We chose the best-fitting model by calculating mean AIC_c weights and AIC_c ranks across all MCC-set and sample-set trees and calculated that model's Nagelkerke pseudo-R² using a single-rate BM model as the null. For most sample-set trees, we could not obtain reliable fits for single rate and single optimum OU models using OUwie (Beaulieu *et al.*, 2012), so we fit these models using Geiger (Harmon *et al.*, 2008) instead.

Testing for rate-opportunity relationships

To test for an effect of climate opportunity on rates of climate niche evolution, we extracted the BM rate component (σ^2) from an OU model in which optima and rates of evolution of PC1 (or PC2) were permitted to vary among islands (OUMV; see Results). We tested for a relationship between evolutionary rate and area and climate heterogeneity using simple linear regressions. Climate heterogeneity and area were log-transformed and σ^2 values, which represent variances, were fourth root-transformed (Hawkins & Wixley, 1986). To account for uncertainty in rate estimates, points were weighted by the inverse, untransformed, standard errors of σ^2 estimates from OUwie. We tested whether area mediated the relationship between rate and

climate heterogeneity by regressing the residuals of a rate–log area regression against climate heterogeneity. We also evaluated whether rates varied with the average species richness per island within a region, rather than area. We did not use multiple regression because of our limited sample size. We used one-tailed tests as our hypothesis specifically predicts a positive relationship between evolutionary rate, climate heterogeneity and area. Recent developments have raised concerns regarding inferences and fits of OU models (Ho & Ane, 2014; Thomas *et al.*, 2014). Thus, we also tested whether relationships between evolutionary rate, area, and climate heterogeneity held under a model of region-specific BM evolution, even though this model was not as well supported as the region-specific OU model.

RESULTS

Models of climate niche evolution

We found no evidence for an exponential decline in the rate of climate niche evolution through time ('early burst', *sensu* Harmon *et al.*, 2010) in any of our regions' major clades (Fig. S2, Tables S3 & S4) for either temperature niche position (PC1) or temperature seasonality (PC2). In general, BM or OU models fit the data better than ACDC models, although accelerating rate ACDC models were indistinguishable from OU models using AIC_c (Table S3; also see Slater *et al.*, 2012). Next, we compared flexible BM and OU models where rates were constrained or permitted to vary across regions, using our reconstructions of *Anolis* colonization history to assign lineages to regions (e.g. Fig. S1). For both temperature niche axes, the best fitting model, even after accounting for missing species and phylogenetic uncertainty, was an OU model with a single 'stabilizing' parameter (α), and multiple region-specific optima (θ) and BM rate (σ^2) components (Table 1). For temperature niche position, this OUMV model (*sensu* Beaulieu *et al.*, 2012) was the best-fitting model for all 50 trees of the MCC-set and had a mean \pm s.d. Nagelkerke pseudo-R² of 0.43 ± 0.09 . For the sample-set, which includes variability both from missing species and phylogenetic uncertainty, OUMV was the best fitting model in 45 of 50 cases (Table 1) and had a mean \pm s.d. Nagelkerke pseudo-R² of 0.37 ± 0.1 . For the temperature seasonality axis, OUMV was the best fitting model in 45 cases for the MCC-set (mean \pm s.d. Nagelkerke pseudo-R² = 0.66 ± 0.02) and 34 cases for the sample-set (mean \pm s.d. Nagelkerke pseudo-R² = 0.60 ± 0.04), respectively (Table 2).

Climate opportunity and climate niche radiation

Using the median of rate estimates from the MCC-set, we found no relationship between the rate of temperature niche position evolution (region-specific σ^2) and climate heterogeneity when area was ignored (Fig. 2a, R² = 0.003, slope \pm s.e. = 0.04 ± 0.32 , $t = 0.11$, $df = 4$, $P = 0.46$). However, despite our small sample size, the rate of temperature niche position evolution was significantly higher in large regions (Fig. 2b, R² = 0.79, slope \pm s.e. = 0.11 ± 0.03 , $t = 3.82$, $df = 4$, $P = 0.009$). As

Table 1 Fit of macroevolutionary models of temperature niche position evolution using Akaike weights and AIC_c ranks (low to high). For both the MCC and sample-sets of trees (50 trees in each), OUMV models fit best. OUMV models are Ornstein-Uhlenbeck models that allowed optima and net rates of evolution to vary among regions.

Model	MCC tree set					Sample-set				
	Akaike weight		AIC _c rank			Akaike weight		AIC _c rank		
	Mean	s.d.	Mode	Min	Max	Mean	s.d.	Mode	Min	Max
BM	1.4×10^{-8}	2.3×10^{-8}	6 (41)	5	6	3.0×10^{-5}	1.0×10^{-4}	6 (33)	4	6
BMM	1.6×10^{-3}	2.9×10^{-3}	2 (38)	2	5	3.6×10^{-2}	1.0×10^{-1}	2 (27)	1	5
OU	1.1×10^{-7}	2.0×10^{-7}	4 (30)	3	5	9.2×10^{-4}	3.2×10^{-3}	4 (29)	2	5
OUM	1.2×10^{-7}	2.8×10^{-7}	4–5 (17)	2	6	5.8×10^{-5}	1.7×10^{-4}	5 (18)	2	6
OUMA	3.2×10^{-5}	2.0×10^{-4}	3 (27)	2	6	3.2×10^{-5}	2.1×10^{-1}	3 (19)	1	6
OUMV	1.0	2.3×10^{-3}	1 (50)	1	1	8.9×10^{-1}	2.3×10^{-1}	1 (45)	1	2

Note: Parentheses give the number of trees with the modal value. The MCC tree set was composed of 50 trees each composed of the maximum clade credibility (MCC) tree with missing species added in a constrained random fashion. The sample-set of 50 trees was randomly chosen from a larger set of 898 trees drawn from the posterior distribution of trees. Missing species were added to each tree in a constrained random way. BM=single-rate Brownian motion, BMM=multi-rate BM, OU=single-optimum Ornstein-Uhlenbeck, OUM=multi-optima OU, OUMA=OUM with free stabilizing parameter (α), OUMV=OUM with free net rate parameter (σ^2). OUM models with both parameters free (OUMVA) were excluded because reliable solutions could not be obtained.

Table 2 Fit of macroevolutionary models of temperature niche seasonality evolution using Akaike weights and AIC_c ranks (low to high). For both the MCC and sample-sets of trees (50 trees in each), OUMV models fit best. OUMV models are Ornstein-Uhlenbeck models that allowed optima and net rates of evolution to vary among regions.

Model	MCC tree set					Sample-set				
	Akaike weight		AIC _c rank			Akaike weight		AIC _c rank		
	Mean	s.d.	Mode	Min	Max	Mean	s.d.	Mode	Min	Max
BM	8.3×10^{-22}	4.7×10^{-21}	4 (46)	4	6	1.7×10^{-16}	1.1×10^{-15}	4 (38)	3	6
BMM	1.8×10^{-1}	1.6×10^{-1}	2 (45)	1	2	3.1×10^{-1}	3.5×10^{-1}	2 (33)	1	3
OU	6.3×10^{-22}	4.0×10^{-21}	5 (48)	5	6	6.2×10^{-17}	3.9×10^{-16}	5 (37)	4	6
OUM	3.4×10^{-22}	2.3×10^{-21}	6 (46)	4	6	9.7×10^{-16}	6.8×10^{-15}	6 (36)	3	6
OUMA	5.7×10^{-8}	2.5×10^{-7}	3 (50)	3	3	3.5×10^{-2}	1.7×10^{-1}	3 (43)	1	6
OUMV	8.2×10^{-1}	1.6×10^{-1}	1 (45)	1	2	6.6×10^{-1}	3.7×10^{-1}	1 (34)	1	2

Note: Parentheses give the number of trees with the modal value. The MCC tree set was composed of 50 trees each composed of the maximum clade credibility (MCC) tree with missing species added in a constrained random fashion. The sample-set of 50 trees was randomly chosen from a larger set of 898 trees drawn from the posterior distribution of trees. Missing species were added to each tree in a constrained random way. BM=single-rate Brownian motion, BMM=multi-rate BM, OU=single-optimum Ornstein-Uhlenbeck, OUM=multi-optima OU, OUMA=OUM with free stabilizing parameter (α), OUMV=OUM with free net rate parameter (σ^2). OUM models with both parameters free (OUMVA) were excluded because reliable solutions could not be obtained.

predicted, the residuals of the rate – area regression were positively related to climate heterogeneity, indicating that for a given area, temperature niche position radiates more quickly in the presence of substantial climate heterogeneity (Fig. 2c, $R^2 = 0.77$, slope \pm s.e. = 0.26 ± 0.07 , $t = 3.71$, d.f. = 4, $P = 0.01$). Missing species did not influence these results: all 50 trees in the MCC-set produced identical regression models in terms of slope direction and significance (not shown). Our findings were also robust to phylogenetic uncertainty. For the sample-set, the rate of temperature niche position evolution was unrelated to heterogeneity for all 50 trees, positively related to area for 48 trees, and the

residuals of the rate-area relationship were positively related to climate heterogeneity for 39 of 50 trees. Our results also held under a multi-rate Brownian motion model (Fig. S3): the rate of evolution was not significantly related to climate heterogeneity ($P > 0.2$), but increased significantly with area ($P < 0.02$) for all 50 trees in the MCC-set. The residuals of the Brownian motion model rate – area regression were also significantly related to heterogeneity for 39 trees.

For the temperature seasonality axis, using the medians of region-specific σ^2 in the MCC-set, we found no relationship between evolutionary rate and climate heterogeneity (Fig. 3a,

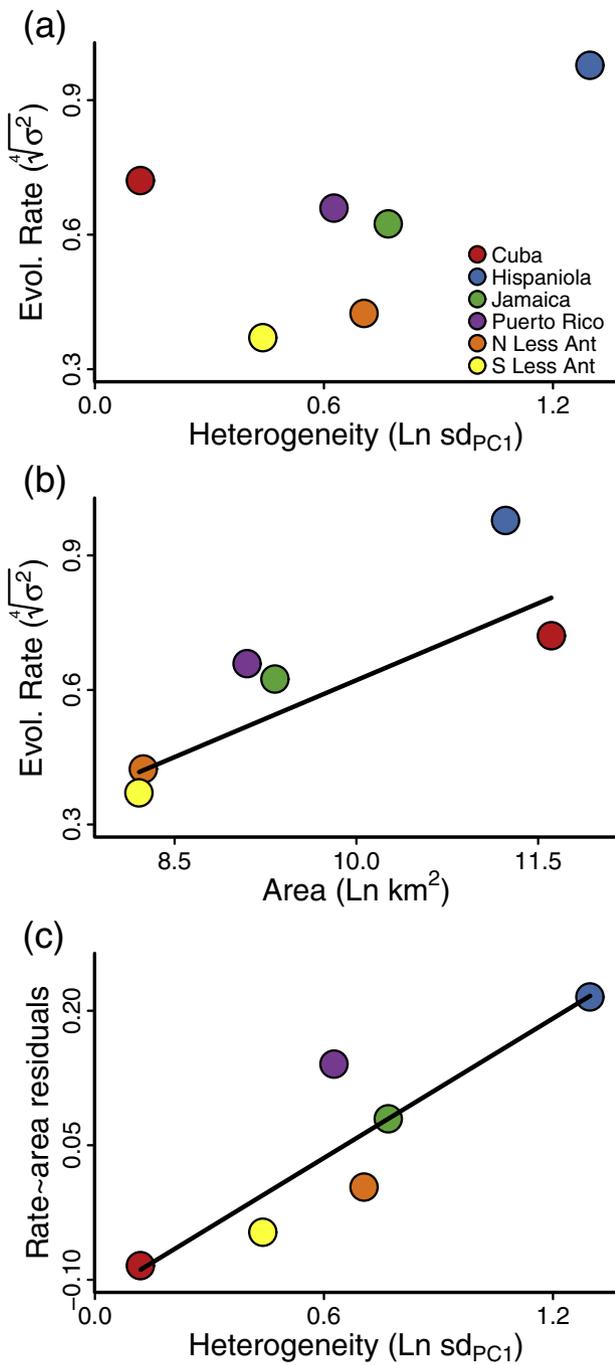


Figure 2 Rates of temperature niche position evolution in relation to climate heterogeneity (a), and area (b). (c) depicts the area-corrected rate – heterogeneity relationship, obtained by regressing the residuals of (b) on heterogeneity. Evolutionary rates are the median net rates (σ^2) from the MCC-set of trees for Ornstein-Uhlenbeck models with a single stabilizing parameter and varying net rates across regions. The MCC-set of trees was composed of 50 trees, each composed of the maximum clade credibility (MCC) tree with missing species added randomly to branches within their known taxonomic subclades. Heterogeneity was measured as the standard deviation of PC scores. (a) is not statistically significant ($P = 0.46$) but (b) and (c) are ($P \leq 0.01$).

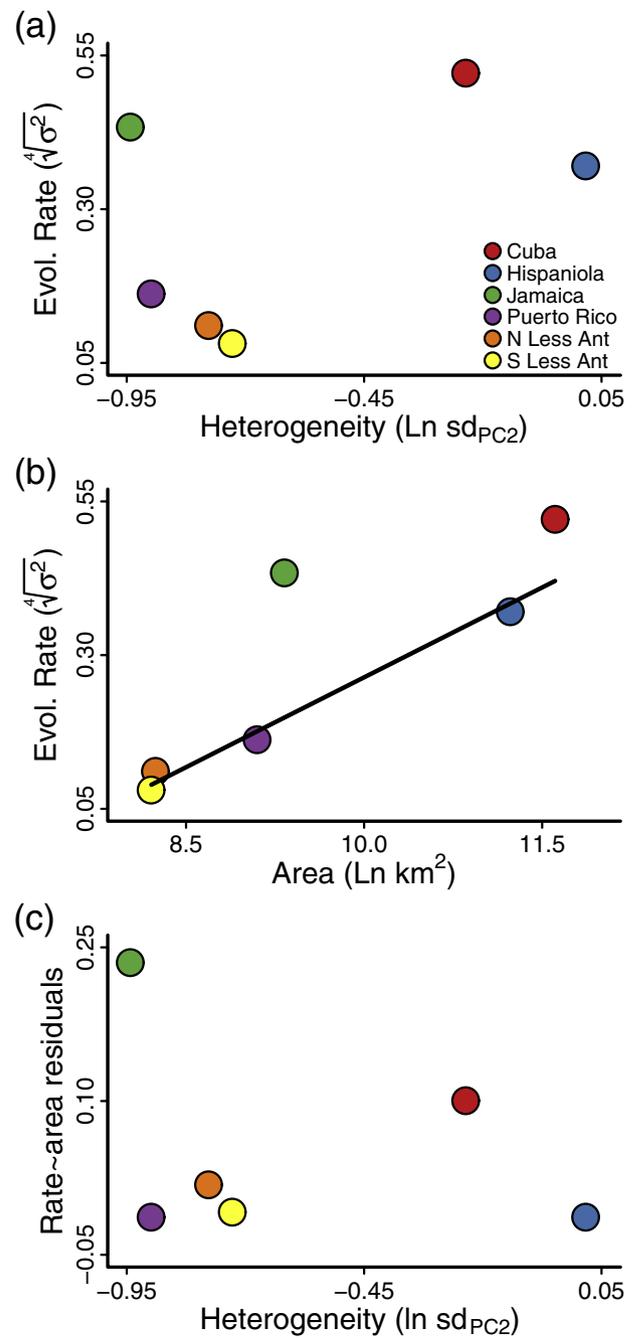


Figure 3 Rates of temperature niche seasonality evolution in relation to climate heterogeneity (a), and area (b). (c) depicts the area-corrected rate – heterogeneity relationship, obtained by regressing the residuals of (b) on heterogeneity. Evolutionary rates are the median net rates (σ^2) from the MCC-set of trees for Ornstein-Uhlenbeck models with a single stabilizing parameter and varying net rates across regions. The MCC-set of trees was composed of 50 trees, each composed of the maximum clade credibility (MCC) tree with missing species added in a constrained random fashion. Heterogeneity was measured as the standard deviation of PC scores. (a) and (c) are not statistically significant ($P \geq 0.30$) but (b) is ($P = 0.005$).

$R^2 = 0.03$, slope \pm s.e. = 0.09 ± 0.24 , $t = 0.36$, d.f. = 4, $P = 0.37$) and a positive relationship with area (Fig. 3b, $R^2 = 0.84$, slope \pm s.e. = 0.10 ± 0.02 , $t = 4.52$, d.f. = 4, $P = 0.005$). However, unlike for temperature niche position, there was still no relationship with climate heterogeneity after accounting for area (Fig. 3c, $R^2 = 0.07$, slope \pm s.e. = -0.07 ± 0.12 , $t = -0.56$, d.f. = 4, $P = 0.30$). Results were also robust to missing species and phylogenetic uncertainty. Regression results were identical in terms of direction and significance for all 50 trees in the MCC-set; for the sample-set the relationship between evolutionary rate and climate heterogeneity was not significant for 47 trees, the evolutionary rate – area relationship was significant for 42 trees, and rate – area residuals were not related to climate heterogeneity for any trees. Results were nearly identical when rates were measured using a multi-rate Brownian motion model (Fig. S4), and were similarly robust to missing species and phylogenetic uncertainty (not shown).

We also tested whether the relationships we found between evolutionary rate and area could have arisen because larger areas harbour higher species richness, which could increase competitive interactions, promoting niche divergence. We regressed the evolutionary rate of mean temperature niche position on the mean number of species per island (log-transformed) within a region and found a significant positive relationship (Fig. 4, $P < 0.05$ for all trees in the MCC and sample-sets). For rates of temperature seasonality evolution, results were similar (Fig. 4, $P < 0.05$ for all trees in the MCC-set and 41 of 50 trees in the sample-set). These results are hardly surprising as mean island species richness and region area are highly correlated (Pearson's $r = 0.97$, d.f. = 4, $P < 0.002$; Fig. S5). This high collinearity and our small sample size prohibited the use of multiple regression to evaluate the independent and shared contributions of area and mean species richness to the rate of climate niche evolution.

DISCUSSION

We hypothesised that ecological opportunity at biogeographic scales determines where clades fall on the continuum from climate niche conservatism to rapid radiation. We tested this hypothesis by asking whether rates of temperature niche diversification in Caribbean *Anolis* were faster in larger and more climatically heterogeneous regions. We found that the rate of climate niche evolution primarily depended on the geographical area available for radiation. Area is well known to influence both species richness and species diversification on islands (Losos & Schluter, 2000; Wagner *et al.*, 2014). The consistent responses of temperature niche position and seasonality evolution to geographical area indicate that area is also fundamentally important for climate niche radiation, influencing whether clades successfully exploit available climate opportunities.

Area may affect rates of climatic niche evolution either directly or indirectly. If areas are too small, then speciation cannot occur, which obviously prohibits radiation (Losos & Schluter, 2000; Kisel & Barraclough, 2010; Losos, 2010; Losos & Mahler, 2010). However, speciation itself is no guarantee that a lineage will diversify along climate niche axes. For example,

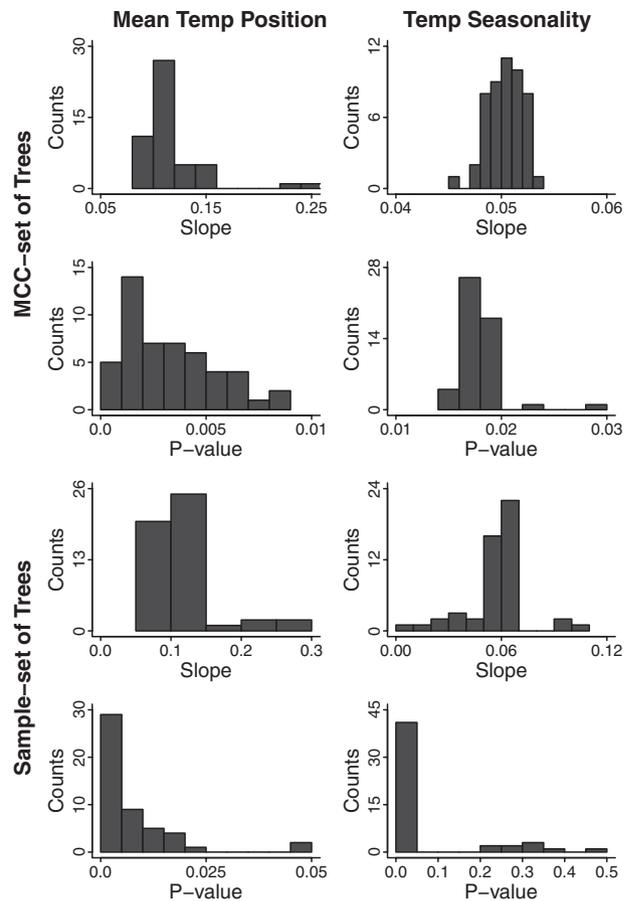


Figure 4 Slopes and P-values of the relationship between the rate of temperature niche evolution and the average number of species per island within a region for the MCC- and sample-sets of trees. The MCC-set of trees was composed of 50 trees, each composed of the maximum clade credibility (MCC) tree with missing species added randomly to branches within their known taxonomic subclades. The sample-set of trees was composed of 50 trees randomly chosen from a larger sample of 898 trees from the Bayesian posterior distribution of chronograms, with missing species added using the same method as the MCC-set.

climate heterogeneity could generate environmental barriers leading to allopatric speciation with little or no niche divergence (niche conservatism; Hua & Wiens, 2013), or it could lead to the evolution of widespread climate generalists, whose ranges and niches broadly overlap. We suggest that large areas allow for 1) speciation and 2) climate specialization along environmental gradients, such as mountainsides, which can result in high rates of climate niche divergence (Hua & Wiens, 2013), either during the speciation process itself, or because of post-speciation adaptation. In small regions, existing climate gradients may not result in the diversification of climate specialists because high gene flow across short geographic distances may prevent speciation from occurring (Doebeli & Dieckmann, 2003). Additionally, climate specialists that did manage to arise in geographically restricted regions would be limited to a subset of conditions

within an already limited area and thus may suffer higher extinction rates due to their small ranges (Gaston, 1998; Cornell, 2013).

Area could also indirectly influence climate niche evolution, via species richness. Larger, more heterogeneous islands host more anole species (Losos & Schluter, 2000), potentially leading to greater competitive pressure that could drive faster climate niche diversification. Consistent with this hypothesis, we found a significant correlation between the average number of species per island and the rate of climate niche evolution. Unfortunately, we were unable to statistically disentangle the direct and indirect effects of area because our sample size is small, and island area and richness are strongly correlated. However, although species richness and strong interspecific competition may partially mediate the relationship between area and climate niche evolution, they are unlikely to be wholly responsible. On large, species-rich Caribbean islands, much of the diversity in climate specialization within clades is partitioned allo- and parapatrically among climatically distinct regions (Losos, 2009). Also, even on the small single-species islands of the Lesser Antilles, there appears to be no shortage of diversifying selection on climate-related niche traits, despite the absence of competition from other anole species. For example, both *A. roquet* and *A. marmoratus* have experienced selection and undergone local climate adaptation within Martinique and Guadeloupe, respectively, but have not successfully speciated within these small islands (Thorpe *et al.*, 2010; Muñoz *et al.*, 2013). Instead, speciation on the Lesser Antilles has occurred between islands. Because these islands are climatically similar to each other, rates of climate niche divergence among their species are low. This lack of divergence highlights the importance of having sufficient area to allow for speciation with climate specialization along environmental gradients, regardless of whether the latter occurs during or after speciation.

We also found evidence of a role for climate heterogeneity in shaping rates of climate niche evolution, but only for one of the two climate niche axes we analysed. Several authors have suggested that increased climate heterogeneity should allow for higher rates of climate niche evolution (Evans *et al.*, 2009; Schnitzler *et al.*, 2012; Lawson & Weir, 2014); this expectation can be derived from ecological opportunity theory which proposes that clades radiate to take advantage of underutilized resources or unoccupied niche space (Simpson, 1953; Schluter, 2000; Glor, 2010; Losos, 2010; Losos & Mahler, 2010; Yoder *et al.*, 2010). We found that the relationships between climate opportunity and rates of climate niche radiation are weaker and more variable than relationships with area. Perhaps surprisingly, climate heterogeneity was not by itself a significant predictor of evolutionary rate. However, for temperature niche position, climate heterogeneity explained residual variation in the rate of temperature evolution, once the effect of area was accounted for. Thus, for the most variable climate niche axis in our data set, we found evidence consistent with the joint influence of area and climate heterogeneity on rates of climate niche evolution. The relative importance of these two factors can be understood by considering patterns of temperature niche evolution on the islands of

Cuba and Hispaniola. Cuba exhibited the second highest rate of temperature niche position evolution in our data set, after Hispaniola. Although Cuba contains mountainous areas, it is dominated by lowlands and thus harbours less overall temperature heterogeneity than any of the other island groups (Figs 1a & 2a). After accounting for its large area, Cuba had a substantial deficit in its rate of temperature niche position radiation, as predicted by the relative lack of climate opportunities. In contrast, Hispaniola, which is both large and considerably more heterogeneous, harboured the highest rates of temperature niche position evolution. Thus, while area explains much of the variation in temperature niche evolution in Caribbean anoles, climate heterogeneity can explain why individual islands have lower or higher rates of temperature evolution than predicted by area alone.

The spatial structure of climate heterogeneity, as well as its extent, may play a role in climate niche radiation. We only examined spatially-implicit climate heterogeneity, which includes no information on the clustering or location of climatic conditions (Wiens, 2000). Given that speciation and climate niche evolution are spatial processes, spatially-explicit heterogeneity, i.e., the spatial clustering and position of different climate zones (Wiens, 2000), may further influence rates of climate niche evolution. For example, Hispaniola had the highest rate of temperature niche position evolution and it also contains several large, distinct highland areas, in contrast to Cuba, which contains less highland area (Muñoz *et al.*, 2014b). Multiple high elevation specialists have evolved on each Hispaniolan mountain range (Wollenberg *et al.*, 2013; Muñoz *et al.*, 2014a), suggesting that the replicated, large, climate gradients on Hispaniola may have contributed to its available climate opportunities.

The differing responses of species' positions along the temperature and seasonality axes to climate heterogeneity – after correcting for area – indicates that additional factors influence whether clades radiate along particular niche axes. Previous studies have demonstrated that rates of evolution for seasonality niche axes can have different dynamics than those for temperature position (e.g. Fisher-Reid *et al.*, 2012). However, we can still only speculate as to why the temperature seasonality axis did not radiate as a function of climate heterogeneity. Losos & Mahler (2010) and Losos (2010) summarized four reasons for why clades may fail to radiate in the presence of ecological opportunity: 1) a lack of speciation, 2) low evolvability, 3) inability to access resources, and 4) misperception of opportunity. Of these, we can discount a lack of speciation, as anoles have speciated extensively on larger islands. We think low evolvability is also unlikely as, in at least some Hispaniolan anoles, thermal tolerance breadth can evolve relatively quickly along elevational gradients (Muñoz *et al.*, 2014a). An inability to access niche space may contribute: though anoles occur in all environments in the Caribbean, it is possible that the spatial structure of seasonality prohibits rapid divergence and specialization along this niche axis. It is also possible that we have misclassified the amount of opportunity for radiation along the temperature seasonality niche axis in the Caribbean. Because the Greater and Lesser Antilles occur within a relatively narrow latitudinal band, there may be insufficient spatial variation in seasonality to stimulate

radiation. To better understand the relationship between climate heterogeneity and rates of evolution in the seasonality niche, it will likely be necessary to turn to other systems.

Our correlative study leaves open the possibility that rates of climatic niche evolution are not constrained by area, species richness and/or climate heterogeneity *per se*, but rather by an unmeasured covariate, such as habitat diversity. However, this seems unlikely for Caribbean *Anolis*. On the Greater Antilles, where anoles have diversified to the greatest extent to specialize on various structural microhabitats, climate and microhabitat specialization are biogeographically and evolutionarily decoupled (Williams, 1972; Hertz *et al.*, 2013). Anole habitat specialists (e.g. grass-bush or trunk ecomorph anoles) tend to be distributed island-wide rather than restricted to a particular climatic region. Also, habitat diversification in Greater Antillean *Anolis* occurred early during these island radiations (Mahler *et al.*, 2010, 2013), with most of the evolutionary transitions in climate specialization occurring later, as populations of wide-spread microhabitat specialists become geographically and reproductively isolated and subsequently adapted to local climatic conditions (Hertz *et al.*, 2013).

Adaptive radiation in the presence of ecological opportunity predicts an early-burst of niche evolution (Glor, 2010; Harmon *et al.*, 2010; Mahler *et al.*, 2010), but we observed no such decline in the rate of evolution along either temperature niche axis. Instead, we found patterns consistent with either an OU model of evolution or an accelerating rate, two models that cannot be distinguished statistically using standard comparative tools (Slater *et al.*, 2012). We cannot exclude the possibility that the lack of an early burst of climate niche evolution is due to difficulty in detecting such patterns (Slater & Pennell, 2014), nor does the good fit of OU models mean that temperature niche traits are under stabilizing selection (Thomas *et al.*, 2014). However, the lack of support for early-burst models likely reflects real differences in how climate niches radiate, compared to other ecological niche axes. Ecological opportunity has traditionally been concerned with niche axes relating to locally consumable resource use (e.g. food, territories) for which organisms compete at the individual level (Schluter, 2000). Alternatively, large scale climate zones, unlike food or microhabitats, are not a directly consumable resource for which individuals directly compete (Keller & Seehausen, 2012). Rather, such zones contain consumable resources that are available to populations that can overcome the challenges posed by novel climate conditions. This degree of separation from direct competition, coupled with their large size, could mean that climate zones may be less easily 'depleted' than food resources or microhabitats [though even regional species assemblages may, eventually, become at least partly saturated (Cornell, 2013)]. Additionally, as mentioned above, anoles partitioned non-climate ecological opportunities (microhabitats) during an early burst of ecomorphological diversification (Mahler *et al.*, 2010, 2013), and climate divergence may have begun only after such opportunities diminished (Williams, 1972; Hertz *et al.*, 2013).

Our analysis was limited to six island regions. Thus our inferences must be tempered by the small sample size available for

statistical analyses. On the one hand, the fact we recovered statistical significance with such a low sample size suggests that the relationships may be quite strong. On the other hand, with so few data, each datum can potentially exert a strong influence on regression results, increasing the chances of a spurious relationship. Unfortunately, the geography of the Caribbean limited our sample size, even after we relaxed the definition of region to group nearby Lesser Antillean islands into conglomerates. Larger sample sizes could be achieved by using clades or species pairs as the units of analyses, rather than geographical regions, and measuring climate heterogeneity and geographical area using a clade's current geographical range (Fisher-Reid *et al.*, 2012; Lawson & Weir, 2014). Although it allows for larger sample sizes, this approach also has disadvantages. Firstly, it requires the arbitrary delineation of clades. Secondly, it quantifies the area and climate opportunities successfully exploited by a clade, rather than those available to it. Our geographical approach allows climate opportunity to be identified *a priori*, which is desirable but often difficult in studies of ecological opportunity (Losos, 2010).

Our understanding of what drives climate niche conservatism and radiation is far from complete. For example, temporal climate variation may also affect climate niche dynamics. Furthermore, we still have limited understanding of whether rates of climate niche evolution reflect adaptation (Boucher *et al.*, 2014), and how underlying thermal traits relate to climate niche limits and geographic climate variation (Lawson & Weir, 2014). Future work may investigate heterogeneity in rates of evolution among clades within a single region (e.g. do clades inhabiting the small Cuban mountainous areas evolve more quickly than lowland Cuban clades?). Lastly, climate zones differ in more than just temperature. They also vary in precipitation, prey availability, and predator and pathogen pressure, suggesting that radiation into new climate zones may require simultaneous evolution along a diversity of niche axes. In summary, considerable opportunity remains to improve our ability to explain why clades fall where they do on the climate niche continuum. Large and isolated islands in the zone of radiation will doubtless play an important role in revealing the factors that open or close opportunities for climate niche radiation.

ACKNOWLEDGEMENTS

J. Losos provided useful suggestions, L. Revell provided help with phytools code and R. Glor provided assistance with occurrence data. The manuscript benefitted greatly from helpful critiques by R. Ricklefs and two anonymous referees. We also thank the Biogeography Research Group of the Royal Geographical Society (with IBG) for providing funding support for ACA to present this research at INTECOL 2013.

REFERENCES

- Algar, A.C. & Losos, J.B. (2011) Evolutionary assembly of island faunas reverses the classic island-mainland richness difference in *Anolis* lizards. *Journal of Biogeography*, **38**, 1125–1137.

- Algar, A.C., Mahler, D.L., Glor, R.E. & Losos, J.B. (2013) Niche incumbency, dispersal limitation and climate shape geographical distributions in a species-rich island adaptive radiation. *Global Ecology and Biogeography*, **22**, 391–402.
- Beaulieu, J.M., Jhwueng, D.-C., Boettiger, C. & O'Meara, B.C. (2012) Modeling stabilizing selection: expanding the Ornstein-Uhlenbeck model of adaptive evolution. *Evolution*, **66**, 2369–2383.
- Boucher, F.C., Thuiller, W., Davies, T.J. & Lavergne, S. (2014) Neutral biogeography and the evolution of climatic niches. *The American Naturalist*, **183**, 573–584.
- Cooper, N., Freckleton, R.P. & Jetz, W. (2011) Phylogenetic conservatism of environmental niches in mammals. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 2384–2391.
- Cornell, H.V. (2013) Is regional species diversity bounded or unbounded? *Biological Reviews*, **88**, 140–165.
- Doebeli, M. & Dieckmann, U. (2003) Speciation along environmental gradients. *Nature*, **421**, 259–264.
- Evans, M.E.K., Smith, S.A., Flynn, R.S. & Donoghue, M.J. (2009) Climate, niche evolution, and diversification of the 'Bird-Cage' evening primroses (*Oenothera*, sections *Anogra* and *Kleinia*). *The American Naturalist*, **173**, 225–240.
- Fisher-Reid, M.C., Kozak, K.H. & Wiens, J.J. (2012) How is the rate of climatic-niche evolution related to climatic-niche breadth? *Evolution*, **66**, 3836–3851.
- Gaston, K.J. (1998) Species-range size distributions: products of speciation, extinction and transformation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **353**, 219–230.
- Glor, R.E. (2010) Phylogenetic insights on adaptive radiation. *Annual Review of Ecology, Evolution, and Systematics*, **41**, 251–270.
- Harmon, L.J., Weir, J.T., Brock, C.D., Glor, R.E. & Challenger, W. (2008) geiger: analysis of evolutionary diversification. *Bioinformatics*, **24**, 129–131.
- Harmon, L.J., Losos, J.B., Davies, T.J., Gillespie, R.G., Gittleman, J.L., Jennings, W.B., Kozak, K.H., McPeck, M.A., Moreno-Roark, F., Near, T.J., Purvis, A., Ricklefs, R.E., Schluter, D., Schulte, J.A., Seehausen, O., Sidlauskas, B.L., Torres-Carvajal, O., Weir, J.T. & Mooers, A.O. (2010) Early bursts of body size and shape evolution are rare in comparative data. *Evolution*, **64**, 2385–2396.
- Hawkins, D.M. & Wixley, R.A.J. (1986) A note on the transformation of chi-squared variables to normality. *The American Statistician*, **40**, 296–298.
- Hertz, P.E., Arima, Y., Harrison, A., Huey, R.B., Losos, J.B. & Glor, R.E. (2013) Asynchronous evolution of physiology and morphology in *Anolis* lizards. *Evolution*, **67**, 2101–2113.
- Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G. & Jarvis, A. (2005) Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology*, **25**, 1965–1978.
- Ho, L.S.T. & Ane, C. (2014) Intrinsic inference difficulties for trait evolution with Ornstein-Uhlenbeck models. *Methods in Ecology and Evolution*, **5**, 1133–1146.
- Hua, X. & Wiens, J.J. (2013) How does climate influence speciation? *The American Naturalist*, **182**, 1–12.
- Ingram, T. (2011) Speciation along a depth gradient in a marine adaptive radiation. *Proceedings of the Royal Society B: Biological Sciences*, **278**, 613–618.
- Keller, I. & Seehausen, O. (2012) Thermal adaptation and ecological speciation. *Molecular Ecology*, **21**, 782–799.
- Kisel, Y. & Barraclough, T.G. (2010) Speciation has a spatial scale that depends on levels of gene flow. *The American Naturalist*, **175**, 316–334.
- Kozak, K.H. & Wiens, J.J. (2010) Accelerated rates of climatic-niche evolution underlie rapid species diversification. *Ecology Letters*, **13**, 1378–1389.
- Lawson, A.M. & Weir, J.T. (2014) Latitudinal gradients in climatic-niche evolution accelerate trait evolution at high latitudes. *Ecology Letters*, **17**, 1427–1436.
- Losos, J.B. (2009) *Lizards in an evolutionary tree: ecology and adaptive radiation of anoles*. University of California Press, Berkeley.
- Losos, J.B. (2010) Adaptive radiation, ecological opportunity, and evolutionary determinism. *The American Naturalist*, **175**, 623–639.
- Losos, J.B. & Mahler, D.L. (2010) Adaptive radiation: the interaction of ecological opportunity, adaptation, and speciation. *Evolution since Darwin: the first 150 years*. (ed. by M.A. Bell, D.J. Futuyma, W.F. Eanes and J.S. Levinton), pp. 381–420. Sinauer Associates, Sunderland, MA.
- Losos, J.B. & Schluter, D. (2000) Analysis of an evolutionary species-area relationship. *Nature*, **408**, 847–850.
- Mahler, D.L., Revell, L.J., Glor, R.E. & Losos, J.B. (2010) Ecological opportunity and the rate of morphological evolution in the diversification of Greater Antillean anoles. *Evolution*, **64**, 2731–2745.
- Mahler, D.L., Ingram, T., Revell, L.J. & Losos, J.B. (2013) Exceptional convergence on the macroevolutionary landscape in island lizard radiations. *Science*, **341**, 292–295.
- Muñoz, M.M., Crawford, N.G., McGreevy, T.J., Messana, N.J., Tarvin, R.D., Revell, L.J., Zandvliet, R.M., Hopwood, J.M., Mock, E., Schneider, A.L. & Schneider, C.J. (2013) Divergence in coloration and ecological speciation in the *Anolis marmoratus* species complex. *Molecular Ecology*, **22**, 2668–2682.
- Muñoz, M.M., Stimola, M.A., Algar, A.C., Conover, A., Rodriguez, A.J., Landestoy, M.A., Bakken, G.S. & Losos, J.B. (2014a) Evolutionary stasis and lability in thermal physiology in a group of tropical lizards. *Proceedings of the Royal Society B: Biological Sciences*, **281**, 20132433.
- Muñoz, M.M., Wegener, J.E. & Algar, A.C. (2014b) Untangling intra- and interspecific effects on body size clines reveals divergent processes structuring convergent patterns in *Anolis* lizards. *The American Naturalist*, **184**, 636–646.
- Revell, L.J. (2012) phytools: an R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, **3**, 217–223.
- Ricklefs, R. & Bermingham, E. (2008) The West Indies as a laboratory of biogeography and evolution. *Philosophical*

- Transactions of the Royal Society of London B: Biological Sciences*, **363**, 2393–2413.
- Schluter, D. (2000) *The ecology of adaptive radiation*. Oxford University Press, Oxford.
- Schnitzler, J., Graham, C.H., Dormann, C.F., Schifffers, K. & Linder, H.P. (2012) Climatic niche evolution and species diversification in the Cape flora, South Africa. *Journal of Biogeography*, **39**, 2201–2211.
- Schwartz, A. & Henderson, R.W. (1991) *Amphibians and reptiles of the West Indies: descriptions, distributions, and natural history*. University of Florida Press, Gainesville, FL.
- Seehausen, O. (2006) African cichlid fish: a model system in adaptive radiation research. *Proceedings of the Royal Society B: Biological Sciences*, **273**, 1987–1998.
- Simpson, G.G. (1953) *The major features of evolution*. Columbia University Press, New York.
- Slater, G.J. & Pennell, M.W. (2014) Robust regression and posterior predictive simulation increase power to detect early bursts of trait evolution. *Systematic Biology*, **63**, 293–308.
- Slater, G.J., Harmon, L.J. & Alfaro, M.E. (2012) Integrating fossils with molecular phylogenies improves inference of trait evolution. *Evolution*, **66**, 3931–3944.
- Smith, S.A. & Beaulieu, J.M. (2009) Life history influences rates of climatic niche evolution in flowering plants. *Proceedings of the Royal Society B: Biological Sciences*, **276**, 4345–4352.
- Thomas, G.H., Cooper, N., Venditti, C., Meade, A. & Freckleton, R.P. (2014) Bias and measurement error in comparative analyses: a case study with the Ornstein Uhlenbeck model. *bioRxiv*, doi: 10.1101/004036.
- Thorpe, R.S., Surget-Groba, Y. & Johansson, H. (2010) Genetic tests for ecological and allopatric speciation in anoles on an island archipelago. *PLoS Genetics*, **6**, e1000929.
- Wagner, C.E., Harmon, L.J. & Seehausen, O. (2014) Cichlid species-area relationships are shaped by adaptive radiations that scale with area. *Ecology Letters*, **17**, 583–592.
- Wiens, J. (2000) Ecological heterogeneity: an ontogeny of concepts and approaches. *The ecological consequences of environmental heterogeneity*. (ed. by M.J. Hutchings, E.A. John and A.J.A. Stewart), pp. 9–31. Blackwell Science Ltd, Oxford.
- Wiens, J.J., Ackerly, D.D., Allen, A.P., Anacker, B.L., Buckley, L.B., Cornell, H.V., Damschen, E.I., Davies, T.J., Grytnes, J.A., Harrison, S.P., Hawkins, B.A., Holt, R.D., McCain, C.M. & Stephens, P.R. (2010) Niche conservatism as an emerging principle in ecology and conservation biology. *Ecology Letters*, **13**, 1310–1324.
- Williams, E.E. (1972) The origin of faunas. Evolution of lizard congeners in a complex island fauna: a trial analysis. *Evolutionary Biology*, **6**, 47–89.
- Wollenberg, K.C., Wang, I.J., Glor, R.E. & Losos, J.B. (2013) Determinism in the diversification of Hispaniolan trunk-ground anoles (*Anolis cybotes* species complex). *Evolution*, **67**, 3175–3190.
- Yang, Z., Kumar, S. & Nei, M. (1995) A new method of inference of ancestral nucleotide and amino acid sequences. *Genetics*, **141**, 1641–1650.
- Yoder, J.B., Clancey, E., Des Roches, S., Eastman, J.M., Gentry, L., Godsoe, W., Hagey, T.J., Jochimsen, D., Oswald, B.P., Robertson, J., Sarver, B.A.J., Schenk, J.J., Spear, S.F. & Harmon, L.J. (2010) Ecological opportunity and the origin of adaptive radiations. *Journal of Evolutionary Biology*, **23**, 1581–1596.

SUPPORTING INFORMATION

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

Appendix S1 Occurrence localities for 139 anole species.

Appendix S2 Accounting for uncertainty in biogeographic reconstruction.

Table S1 Principal component analysis of Worldclim temperature variables.

Table S2 Missing species and their taxonomic affinities.

Table S3 Macroevolutionary model comparisons for major clades on each island for temperature niche position (PC1).

Table S4 Macroevolutionary model comparisons for major clades on each island for the temperature seasonality niche axis (PC2).

Figure S1 Exemplar maximum likelihood reconstruction of anole biogeographic history.

Figure S2 Phylogenies of the major clades on each island.

Figure S3 Evolutionary rate of temperature niche position, area and heterogeneity relationships under Brownian motion.

Figure S4 Evolutionary rate of temperature seasonality, area and heterogeneity relationships under Brownian motion.

Figure S5 Relationship between average island species richness per region and area.

BIOSKETCHES

Dr. Adam C. Algar's research asks how organisms respond ecologically and evolutionarily to climate across spatial scales. He also appreciates a good haiku: 'Life at global scales/Oh collinearity/Regression be damned'.

Dr. D. Luke Mahler's research investigates how ecology shapes the evolution of phenotypic diversity during diversification.

Editor: Robert Ricklefs