



# Evolutionary assembly of island faunas reverses the classic island–mainland richness difference in *Anolis* lizards

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## ABSTRACT

**Aim** Islands are widely considered to be species depauperate relative to mainlands but, somewhat paradoxically, are also host to many striking adaptive radiations. Here, focusing on *Anolis* lizards, we investigate if cladogenetic processes can reconcile these observations by determining if *in situ* speciation can reduce, or even reverse, the classical island–mainland richness discrepancy.

**Location** Caribbean islands and the Neotropical mainland.

**Methods** We constructed range maps for 203 mainland anoles from museum records and evaluated whether geographical area could account for differences in species richness between island and mainland anole faunas. We compared the island species–area relationship with total mainland anole diversity and with the richness of island-sized mainland areas. We evaluated the role of climate in the observed differences by using Bayesian model averaging to predict island richness based on the mainland climate–richness relationship. Lastly, we used a published phylogeny and stochastic mapping of ancestral states to determine if speciation rate was greater on islands, after accounting for differences in geographical area.

**Results** Islands dominated by *in situ* speciation had, on average, significantly more species than similarly sized mainland regions, but islands where *in situ* speciation has not occurred were species depauperate relative to mainland areas. Results were similar at the scale of the entire mainland, although marginally non-significant. These findings held even after accounting for climate. Speciation has not been faster on islands; instead, when extinction was assumed to be low, speciation rate varied consistently with geographical area. When extinction was high, there was some evidence that mainland speciation was faster than expected based on area.

**Main conclusions** Our results indicate that evolutionary assembly of island faunas can reverse the general pattern of reduced species richness on islands relative to mainlands.

## Keywords

*Anolis*, Caribbean islands, climate, diversification rate, evolutionary radiation, island biogeography, reptiles, speciation rate, species richness, species–area relationship.

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## INTRODUCTION

Islands are generally depauperate in species relative to mainland regions, yet they are home to some of nature's most striking adaptive radiations. The low species richness of islands has been attributed both to their generally small size, which increases the likelihood of extinction, and to their isolation, which makes colonization difficult; small size and isolation can also lead to a

reduced range of resources and habitats, further reducing overall species richness (MacArthur & Wilson, 1967; Carlquist, 1974; Lack, 1976). At the same time, the substantial ecological and phenotypic diversity of some clades on islands probably arises from evolutionary radiation into a wealth of empty niches, as proposed by the ecological theory of adaptive radiation (Schluter, 2000). The discrepancy between these patterns results predominantly from the different role that *in situ* evolutionary

diversification plays in these two scenarios. Whereas speciation is a critical component of adaptive radiation, theories explaining the depauperate nature of many islands focus on ecological phenomena and assume, implicitly or explicitly, that cladogenetic speciation does not occur (Heaney, 2000, 2007).

Although MacArthur & Wilson's (1967) highly influential theory of island biogeography discussed evolutionary change on islands, its primary focus was on colonization and extinction dynamics and the huge explosion of subsequent studies generally followed suit. The lack of attention to evolutionary divergence probably resulted because speciation dynamics were assumed to be too slow to compete with immigration and extinction (Heaney, 2000, 2007). However, several recent theoretical and empirical studies have revealed that *in situ* speciation (as opposed to anagenetic change after a dispersal event) can contribute substantially to island richness (Funk & Wagner, 1995; Losos & Schluter, 2000; Mendelson & Shaw, 2005; Parent & Crespi, 2006; Whittaker *et al.*, 2008; Kisel & Barraclough, 2010; Losos & Parent, 2010). More specifically, speciation rate has been shown to vary positively with both island area (Losos & Schluter, 2000; Losos & Parent, 2010) and habitat diversity (Parent & Crespi, 2006). Single-island endemic richness also increases with area (Triantis *et al.*, 2008), although this may not be a good proxy for speciation rate (Whittaker *et al.*, 2008; Chen & He, 2009). However, speciation does not occur on all islands. Rather, there appears to be a minimum island size necessary for speciation (Diamond, 1977; Coyne & Price, 2000; Losos & Schluter, 2000; Kisel & Barraclough, 2010; Losos & Parent, 2010). Thus, on small, oceanic islands, species richness will depend primarily on colonization–extinction dynamics, whereas on larger oceanic islands, cladogenesis will have an increasing influence on island diversity (Losos & Schluter, 2000).

Here we investigate how evolutionary diversification on islands influences the island–mainland species richness difference that has been one of island biogeography's key foci for the past four decades. We predict that small islands, where speciation has not occurred, will conform to the common pattern of reduced diversity relative to that of similar mainland areas. Alternatively, *in situ* speciation on large islands could influence species richness in several ways.

1. If islands can support fewer species than mainlands, then *in situ* speciation will not affect the island–mainland diversity difference and large islands will still have depauperate faunas relative to their area.
2. Substantial *in situ* speciation could result in islands that are essentially small mainlands (as alluded to by Rosenzweig, 1995; Gillespie, 2004; and Kreft *et al.*, 2007). This hypothesis predicts that islands and mainlands will have similar richness and diversification rates after differences in area have been considered.
3. Radiation into empty niches on islands could produce exceptional species richness, resulting in faster diversification and greater species richness than on mainlands.

Climate has been strongly linked to broad-scale species richness gradients on mainlands (e.g. Currie, 1991; Hawkins *et al.*, 2003; Field *et al.*, 2005). Recent work has extended this relationship to islands (Kalmar & Currie, 2006; Kreft *et al.*,

2007). Furthermore, Kalmar & Currie (2007) have shown that, at least for land-birds, climate can account for a portion of the differences among island and mainland richness. Therefore, in addition to area, we also considered the potential effect of climate on island and mainland species richness. Thus, our hypotheses can be more specifically phrased as whether species diversification leads to exceptional, equal or reduced species richness on islands relative to mainlands even after accounting for differences in area and climate.

We test these hypotheses using *Anolis* lizards (Iguanidae) on Caribbean islands and the Neotropical mainland. Anoles have undergone replicate adaptive radiations on each of the four Greater Antillean islands, but, despite inhabiting most Caribbean landmasses, they have not speciated on islands smaller than Puerto Rico (Losos & Schluter, 2000). Anoles have also diversified extensively on the Neotropical mainland (Nicholson *et al.*, 2005; Pinto *et al.*, 2008). In fact, more anole species inhabit the mainland than all Caribbean islands combined (203 vs. 168 according to the Reptile Database, <http://www.reptile-database.org>). The mainland anole fauna is composed of two clades. One is separated from other anoles by the basal split in the anole phylogeny (Nicholson *et al.*, 2005) and inhabits South America and the southern part of Central America; following Pinto *et al.* (2008) we refer to this clade as M1. The second clade, M2, has recently back-colonized the Neotropical mainland from either Jamaica or Cuba (Nicholson *et al.*, 2005) and is distributed throughout Central America and much of South America. Thus, anoles are ideal for testing the role of *in situ* diversification on island richness; there has been sufficient time for diversification on both island and mainland environments and anoles have achieved high diversity on both. Also, because anoles have speciated on only a subset of islands, it is possible to compare the mainland with islands whose faunas have been assembled predominantly by either colonization or by *in situ* diversification.

## MATERIALS AND METHODS

### Mainland and island species richness

Our understanding of *Anolis* taxonomy, like that of many groups, is in a state of flux, with new species being discovered through field collections (e.g. Poe & Yañez-Miranda, 2008; Poe *et al.*, 2008) and morphological analyses (e.g. Köhler & Sunyer, 2008). Here, we considered the 371 species listed by the Reptile Database (<http://www.reptile-database.org>) in late 2009, with one exception. *Anolis altitudinalis* was included as a subspecies of *Anolis isolepis* in the reptile database, but Nicholson *et al.* (2005) found it to be the sister species to *Anolis oporinus*, together forming a sister clade to *A. isolepis*. Thus, we considered it as a distinct species.

To quantify patterns of mainland anole species richness, we generated range maps for 203 species. We did not include island species with limited mainland occurrence records in heavily populated regions that may be the result of recent introductions. We also excluded *Anolis carolinensis* because it is a relatively recent colonist to an area otherwise not naturally inhabited by anoles (Glor *et al.*, 2005).

To build range maps for mainland species, we accessed all *Anolis* (including synonyms, e.g. *Norops*, *Dactyloa*, *Chamaeleolis*) occurrence records from the HerpNet data portal (<http://www.herpnet.org>) and from the Global Biodiversity Information Facility (GBIF; <http://data.gbif.org>). Data were obtained from many institutions (see Appendix S1 in Supporting Information) and were accessed in October 2009. From this set, we assembled a list of all unique localities for each mainland species. Next, we searched the Reptile Database and the Biodiversity Heritage Library (<http://www.biodiversitylibrary.org>) to find papers that potentially contained additional occurrence information (see Appendix S2 for a list of references). The resulting dataset included 4748 unique localities for mainland species, of which approximately 35% had geographical coordinates. Based on the locality description, we manually georeferenced an additional 1929 localities. Ambiguous and contradictory localities (e.g. two towns of the same name within a province) were omitted. While this procedure involved some approximation, at the scale of our study (Central America and much of South America) small georeferencing errors are unlikely to bias our results. For species whose taxonomy has changed (e.g. the description of *Anolis cryptolimifrons* from specimens previously assigned to *Anolis limifrons*; Köhler & Sunyer, 2008), we considered only points that could be unambiguously assigned to a particular species; points that could not be unambiguously assigned to a species were omitted. Our final dataset included 3670 georeferenced occurrences for 203 mainland species.

For species with more than two unique localities, we drew minimum convex polygons (MCPs) around each species' occurrence points. MCPs were then clipped to remove non-land areas, visually examined and adjusted to include adjacent coastal areas that were outside the MCP but seemed likely to form part of the range, e.g. narrow strips of coastline (Fig. S1). For species with two or fewer occurrences, ranges were left as individual points. Köhler (2008) has presented range maps for approximately 90 anoles in Middle America. We did not utilize these maps to maintain consistency with the maps for the other 113 species. However, our maps were broadly concordant with Köhler's (2008) maps. The resulting maps are available from the first author (A.C.A.) as ArcGIS ASCII grids.

To quantify island richness, we used the HerpNet records to generate species tallies for 39 Caribbean islands for which we could obtain relevant environmental data. This approach, as opposed to using previously assembled species lists for the Caribbean, retains consistency with our methods for mainland anoles. The resulting Caribbean richness patterns were essentially indistinguishable from previous publications (e.g. Losos, 1996; Losos & Schluter, 2000).

### Environmental data

To quantify mainland and island environments, we obtained climate and elevation data from WorldClim (<http://www.worldclim.org>; Hijmans *et al.*, 2005). We considered a suite of variables that quantified both mean environmental

values and heterogeneity and seemed likely to influence anole richness: area, elevation range, standard deviation of elevation, mean annual temperature, mean annual temperature range, standard deviation of mean annual temperature, minimum temperature, maximum temperature, temperature seasonality (standard deviation of monthly temperatures), mean annual precipitation, mean annual precipitation range, standard deviation of mean annual precipitation, precipitation seasonality, maximum monthly precipitation and minimum monthly precipitation. Additionally, we also considered net primary production from the MODIS satellite ([https://lpdaac.usgs.gov/lpdaac/products/modis\\_products\\_table](https://lpdaac.usgs.gov/lpdaac/products/modis_products_table)) and land-cover heterogeneity, measured as the number of land-cover types occurring in a region from Global Landcover 2000 (<http://bioval.jrc.ec.europa.eu/products/glc2000/glc2000.php>).

### Analysis

Except where otherwise noted, all analyses were carried out in R 10.2.1 (R Development Core Team 2009) using the *spdep* (Bivand *et al.*, 2009), *geiger* (Harmon *et al.*, 2009), *ape* (Paradis *et al.*, 2004, 2009), *segmented* (Muggeo, 2008) and *laser* (Rabosky, 2009a) packages. Area and species richness were log-transformed for all analyses. Below, we outline the procedure for each of our three main questions.

#### *Are there more or fewer mainland anole species than predicted based on island species–area relationships?*

Losos & Schluter (2000) found that the species–area relationship (SAR) for island anoles has a distinct breakpoint, with richness only weakly related to area for small islands (approximately < 3000 km<sup>2</sup>) and a strong positive linear relationship (on a log scale) for large islands. We repeated this analysis using the breakpoint regression method described by Muggeo (2003), confirming a similar pattern. Next we computed the total area inhabited by mainland anoles by drawing a minimum convex polygon around the complete set of occurrence points for all mainland species. Ideally, we would have preferred to assess the significance of a categorical (island or mainland) term in a linear model. However, given the constraints of a single mainland region, this approach was not possible. Instead, we compared the observed mainland species richness (203 species) with the 95% prediction interval of the large island SAR, with the usual caveats associated with extrapolating outside the data range of a regression. We also compared the fit of all the data (island and mainland) to the island breakpoint model and to a logistic model. The latter allows mainland richness to fall below the linear extrapolation from the island-only relationship.

#### *Can climate and area account for island–mainland subregion richness differences?*

Macroecological studies of mainland species richness gradients usually examine uniformly sized quadrats. Instead, because we

were interested in how area influenced richness, we sampled island-sized subregions of the mainland. We used a spreading-dye model (Jetz & Rahbek, 2001) to delineate a set of mainland subregions (MSRs) based on the observed sizes of islands in our dataset. The spreading-dye model randomly selected an initial location for a MSR, which then expanded randomly outward until a predetermined size was reached. We generated 975 non-overlapping MSRs with each island represented 25 times (Fig. S2). For each MSR, we sampled species richness and the environmental variables described above. Environmental variables for each MSR were determined from the WorldClim 30 arcsec resolution data. For example, mean annual temperature was determined by taking the average of the mean annual temperature for all 30 arcsec cells within the MSR. Richness was calculated as the number of species ranges that overlapped a MSR.

To compare the SARs for islands and MSRs, we first fitted linear and breakpoint regressions (with log-transformed variables) to the MSRs to determine if the overall model form differed from the island SAR. Next, we divided the dataset into small and large areas (based on the island breakpoint) and compared richness within these subsets by determining whether there were significant differences in intercept and slope between islands and MSRs. In addition to significance testing, we also compared models using Akaike's information criterion (AIC) corrected for small sample size (AIC<sub>c</sub>). All analyses were carried out using simultaneous autoregression with an autocorrelated error term (Kissling & Carl, 2008; Beale *et al.*, 2010). The spatial weights matrix was based on the distance ( $d$ ) between MSR (or island) centroids, where the influence of region  $j$  on region  $i$  was calculated as  $1/d_{ij}^\alpha$  (Lichstein *et al.*, 2002), where  $\alpha$  was determined empirically as 1.0 or 2.0, based on the AIC. Regions separated by a distance greater than that at which spatial autocorrelation in species richness became non-significant (based on Moran's  $I$  correlograms) were given weights of zero (Lichstein *et al.*, 2002).

To determine whether climatic differences between islands and the mainland could account for observed species richness differences, we first determined the MSR climate–richness relationship and then applied it to island environments. Model selection for climate–richness relationships can identify numerous models that fit the data indistinguishably well (Dormann *et al.*, 2008). Therefore, we used Bayesian model averaging (BMA; Raftery *et al.*, 1997; Hoeting *et al.*, 1999; Link & Barker, 2006; Dormann *et al.*, 2008) with uniform priors to quantify the mainland climate–richness relationship and to predict island richness. Briefly, BMA combines the predictions from a set of models, which are weighted by their posterior probabilities (Raftery *et al.*, 1997; Hoeting *et al.*, 1999; Link & Barker, 2006). To delineate our prediction set, we first identified a candidate set of models based on the 17 variables mentioned above (transformed as appropriate to improve normality), their quadratic terms and all first-order interactions. Because the number of potential regression models from this set was prohibitively large, we removed variables that were highly collinear (Pearson's  $r > 0.80$ ), retaining the one that was most

strongly correlated with species richness. We also removed those variables that, when combined with their quadratic term, did not explain more than 5% of the variance in species richness. This left a subset of six variables: net primary production, temperature seasonality, minimum temperature, mean annual precipitation, range in mean annual precipitation and minimum monthly precipitation. Adding quadratic terms and first-order interactions resulted in 27 predictors. Following Algar *et al.* (2009), we limited models to a maximum of five independent variables plus an intercept (see also Dormann *et al.*, 2008) and required models that included quadratic and interaction terms to contain the relevant linear terms. This procedure left 743 candidate models, a tractable number given the computational time involved in fitting spatial autoregressive models. We did not use ordinary least squares (OLS) for model selection with subsequent application of spatial regression because Beale *et al.* (2010) found that this procedure routinely selects models that are too long and thus subject to high levels of Type I error. We used 'Occam's window' (Raftery *et al.*, 1997) to identify the prediction set of models. Occam's window selects models that have approximately similar support, given the data, and excludes from this set models that have lower posterior probabilities than their included submodels. Following Raftery *et al.* (1997), we included models with posterior probabilities  $>1/20$ th of the best model's posterior probability in the prediction set.

We used simultaneous autoregression coefficients from the resulting set of models to predict richness in the MSRs and on islands. To determine whether the mainland models could predict island richness as well as mainland richness, we used observed richness as the response variable and the model-averaged predictions as an independent variable in a simultaneous autoregression that also included mainland/island as a categorical variable, where islands were split into two groups depending on whether *in situ* speciation had occurred or not.

#### *Can the island speciation–area relationship predict the mainland speciation rate?*

To compare speciation rates on islands and mainlands, we used Nicholson *et al.*'s (2005) phylogeny of island and mainland *Anolis*. This phylogeny includes most island anoles, but only approximately 25% of mainland species. Nicholson *et al.*'s (2005) phylogeny was based on the mitochondrial ND2 gene, with divergence times estimated using penalized likelihood in r8s (Sanderson, 2003). We randomly resolved polytomies in the Nicholson *et al.* (2005) tree and assigned random branch lengths to the resulting new branches. Because polytomies are likely to be indicative of short branches, we chose random lengths from an exponential distribution with a rate parameter based on the 10% quantile of observed branch lengths. We maintained ultrametricity by subtracting the length of branches subtending a new node from the node's daughter branches. We generated a sample of 50 random trees for subsequent analyses.

Due to the poor sampling of mainland clades, we determined speciation rates on islands and mainlands based on relative

estimates of clade stem age and species richness, assuming either no extinction or a relative extinction rate of 0.90 (Magallon & Sanderson, 2001). Our aim was to estimate a speciation rate for each landmass; when multiple clades were present on an island (or mainland), we found the diversification rate that maximized the likelihood across all clades (Bokma, 2003), using code modified from Rabosky's (2009a) laser package. Losos & Schluter (2000) showed that speciation rates of *Anolis* on small Caribbean islands are essentially zero. Therefore, we considered only those islands with areas greater than the breakpoint area of the island SAR.

To determine the relative age of clades on particular islands, we reconstructed the colonization history of anoles using stochastic character mapping in SIMMAP 1.5 (Bollback, 2006). SIMMAP 1.5 samples ancestral states following the method of Schultz & Churchill (1999). We used a gamma distribution prior whose parameters were fitted using the Markov chain Monte Carlo (MCMC) sampling algorithm in SIMMAP 1.5. We assumed that state transitions along branches indicated dispersal events and that the preceding speciation event was a result of this dispersal. Therefore, clades' stem ages were taken at the base of the branch on which dispersal occurred. For each of the 50 trees, we generated 50 ancestral state reconstructions.

To use stochastic character mapping, species can only be assigned to a single geographical state. Species were coded as occurring on either the mainland, one of the eight islands with areas greater than the island breakpoint (the Greater Antilles, plus Andros, Great Inagua, Isla de la Juventud and Guadeloupe; see Results), or to a synthetic small island category that included all other small Caribbean islands. We assumed that Greater Antillean species that also occurred on smaller Caribbean islands originated on the former and then dispersed to small islands (examples of such species include *Anolis sagrei* and *Anolis distichus*). Because SIMMAP 1.5 limits the possible number of character states to seven, we omitted Great Inagua and Guadeloupe from our ancestral state reconstructions and added these islands (and their endemic species, *Anolis scriptus* on Great Inagua and *Anolis marmoratus* on Guadeloupe) to our dataset after reconstructing ancestral states.

To incorporate missing species into the estimates of diversification rate, we added 56 mainland species to the M1 clade and 96 to M2, based on information in Savage & Guyer (1989), Nicholson *et al.* (2005), Köhler (2008), or the affinities noted by the authors who described the species. On islands, there were far fewer missing species (13 on Cuba, 3 on Hispaniola and 1 on Puerto Rico). We randomly added these species to the species richness of clades inhabiting the relevant island. When more than one clade of mainland M2 (or M1) species was inferred, we randomized the mainland M2 (or M1) species among these clades (in these cases, the additional mainland clade took the form of a single species that was sister to a small island species nested within the larger mainland clade). We performed this randomization 20 times for each ancestral state reconstruction. Thus our analysis was based on 50,000 reconstructions of clade diversities and ages from which

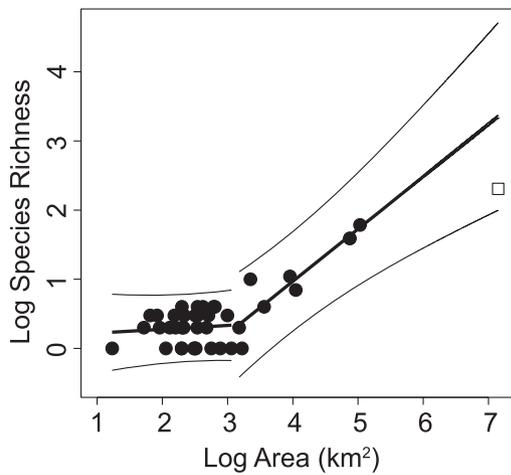
to determine speciation rates (50 trees  $\times$  50 state reconstructions  $\times$  20 missing species randomizations).

For each reconstruction, we determined whether the mainland speciation rate was greater or less than expected based on the island speciation–area relationship identified by Losos & Schluter (2000). We evaluated departure from the island relationship in two ways. First, following our approach for species richness, we determined whether the mainland speciation rate was outside the 95% prediction interval of the island speciation–area relationship. Because this relationship had a wide prediction interval, especially when extrapolated (see Results), we had little power to detect deviations from the island relationship. Therefore, we also compared the slope of the regression lines fitted to all the data and to islands only. If the mainland speciation rate does not deviate substantially from the relationship on islands, then we do not expect these slopes to differ. We computed these comparisons for each of the 50,000 scenarios at both relative extinction rates (0.0 or 0.90).

## RESULTS

### Total mainland richness and the island species–area relationship

We found patterns of island species richness for Caribbean anoles that were almost identical to those of Losos & Schluter (2000; compare our Fig. 1 and their Fig. 3). The data fitted a breakpoint model substantially better than a linear regression of log richness on log area ( $\Delta AIC_c = 10.6$ , where  $\Delta AIC_c = \text{linear } AIC_c - \text{breakpoint } AIC_c$ ) and increased the adjusted  $R^2$  from 0.52 (linear) to 0.68 (breakpoint). For our data, the breakpoint occurred at 1480 km<sup>2</sup> (95% confidence interval: 525–4073 km<sup>2</sup>, analyses performed on log-transformed data). The difference between our breakpoint and the c. 3000 km<sup>2</sup> breakpoint found by Losos & Schluter (2000) probably arose because our dataset includes fewer small, low-diversity islands due the unavailability of climate data for those islands. Extrapolating the island SAR to the mainland area inhabited by anoles ( $1.41 \times 10^7$  km<sup>2</sup>) revealed that mainland richness fell well below the value predicted by the island SAR; it would require thousands of additional mainland species to reach the mean richness predicted by the island SAR. Nonetheless, mainland species richness falls within the 95% prediction interval from the island SAR (Fig. 1). Similar results were found when we limited the mainland region to the latitudinal extent of our island data (not shown). In this case, an additional 378 mainland species would be needed within this latitudinal extent to equal the mean predicted richness from the island relationship. Furthermore, a logistic model fitted to the complete (islands and mainland) dataset had a lower  $AIC_c$  than the island-only breakpoint model extrapolated to include the mainland ( $\Delta AIC_c = 13.6$ ), indicating that a model that allows mainland richness to fall below the linear (on a log-scale) extrapolation from the island relationship provides a better fit to the data than one that does not. The logistic model



**Figure 1** *Anolis* species–area relationship (SAR) for Caribbean islands and the total Neotropical mainland. Islands are closed circles; the mainland is the open square. Narrow lines depict the 95% prediction interval of the island relationship. Island SAR was fitted using breakpoint regression ( $n = 39$ , linear  $AIC_c$  – breakpoint  $AIC_c = 10.6$ , where  $AIC_c$  is Akaike’s information criterion corrected for small sample size).

only slightly over-predicted mainland richness (216 species predicted); however, this is hardly surprising because mainland richness was used to fit the model and due to its large geographical area, has high leverage.

**Climate, area and island and mainland subregion richness**

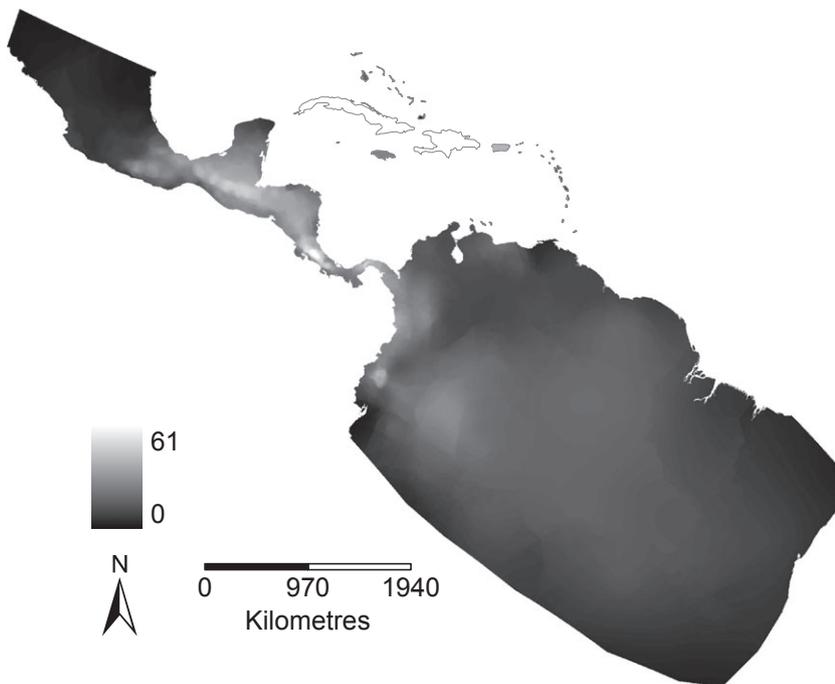
Mainland anole richness peaks in Central America, with high richness in southern Mexico and Panama and especially in Costa

Rica (Fig. 2). In South America, richness was highest in western Colombia. Species richness is generally low throughout the Amazon Basin and the remainder of the range of *Anolis* in South America.

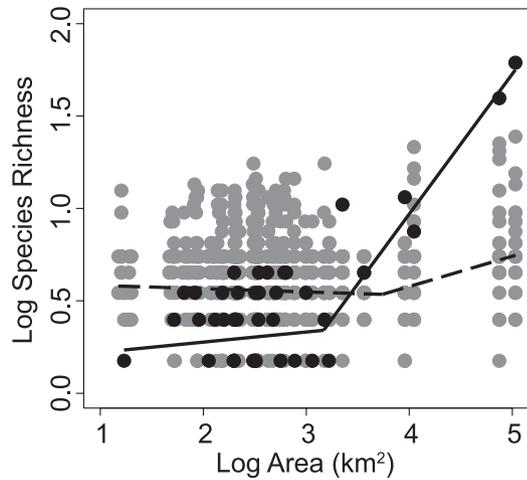
As for the island data, the best fitting model for MSR richness was a breakpoint relationship with area (Fig. 3;  $\Delta AIC_c = 15.2$ ). The island and mainland breakpoints also occurred at similar areas, although their standard errors do not overlap (MSR breakpoint  $\pm$  SE =  $3.74 \pm 0.26$ ; island breakpoint  $\pm$  SE =  $3.17 \pm 0.22$  on a log scale). However, unlike on islands, MSR area only explained 3% of the variance in species richness.

To compare the island and MSR SARs, we fitted simultaneous autoregression models to large ( $\geq 1480$  km<sup>2</sup>, i.e. the island breakpoint) and small areas independently. We note, however, that because richness was only weakly related to MSR area, these regressions essentially compare the diversity of islands with or without *in situ* speciation with the average richness of MSRs, regardless of area. For small areas, islands had significantly fewer species than MSRs, but the island and mainland relationships did not differ in slope, i.e. a statistically significant categorical (island or mainland) variable ( $P < 0.0001$ ), but non-significant interaction with area ( $P > 0.34$ ). However, in large areas, the slope of the SAR was significantly steeper on islands ( $P < 0.001$ ) and richness on the largest islands was greater than on the mainland (Fig. 3). Thus, on large islands, where *in situ* speciation is most important, species richness was higher than in similarly sized mainland areas.

To evaluate whether climate could account for the differences between island and MSR species richness, we planned to use Bayesian model averaging. However, out of > 700 potential models, a single best model (Bayesian information criterion weight > 0.99) was identified:



**Figure 2** Geographical patterns of species richness of Neotropical mainland and Caribbean island anoles shown in greyscale, where white depicts the highest species richness and black the lowest richness. A single value is presented for each island. Mainland richness is spatially smoothed for display purposes only. The map is shown using a Lambert Azimuthal equal-area projection.



**Figure 3** *Anolis* species–area relationships for Caribbean islands (black circles, solid line) and Neotropical mainland subregions (grey circles, dashed line). Species richness is lower on small islands than on the mainland (simultaneous autoregression,  $n = 806$ ,  $P < 0.001$ ), but greater on large islands (simultaneous autoregression,  $n = 208$ ,  $P < 0.001$ ).

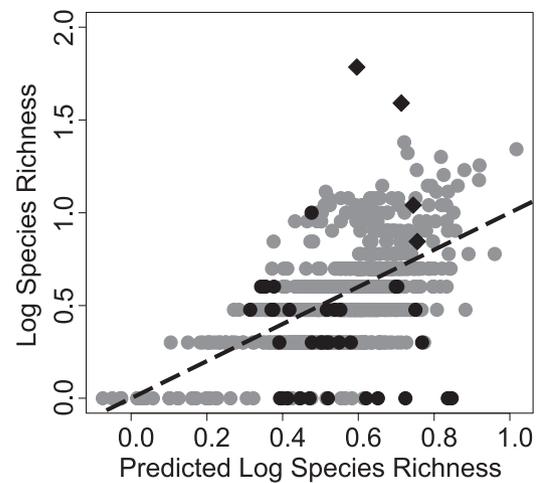
$$\log(\text{SR}) \sim b_0 + b_1 \text{MAP}^{1/3} + b_2 \log(\text{SeasT}) + b_3 \log(\text{SeasT})^2 + b_4 \log(\text{RngMAP}) + b_5 \log(\text{RngMAP})^2 + \varepsilon,$$

where SR is species richness, MAP is mean annual precipitation, RngMAP is the range in mean annual precipitation within an MSR (spatial precipitation heterogeneity), SeasT is temperature seasonality,  $b_i$  are fitted coefficients and  $\varepsilon$  is error. This model explained just over 40% of the variance in MSR richness (pseudo- $R^2$ , based on the regression of observed MSR richness on predicted MSR richness). Area was not included in this model, which is unsurprising as it was weakly related to MSR richness (Fig. 3).

Including MSRs and islands where *in situ* speciation has occurred in a linear model, with the predictions from the mainland climate model as a predictor, revealed that the latter have a different relationship with climate than MSRs (interaction term between MSRs and islands with speciation,  $P < 0.001$ ; Fig. 4). A similar result was found for islands without speciation when compared with mainland regions (interaction term,  $P < 0.001$ ; Fig. 4). Constraining the slopes to be equal (removing the interaction term), revealed that richness on islands with speciation is, on average, higher than mainland richness ( $P < 0.001$ ), a relationship that was driven primarily by Cuba and Hispaniola. However, on islands without speciation, richness was reduced relative to mainlands ( $P < 0.001$ ). Together these results suggest that island biotas are not affected by climate in the same way as mainland biotas and that *in situ* speciation results in elevated richness on islands relative to mainland regions with matching climates.

### Speciation–area relationship on islands and mainlands

Across all 50,000 reconstructions of phylogeny, colonization history and species richness, speciation rate generally increased



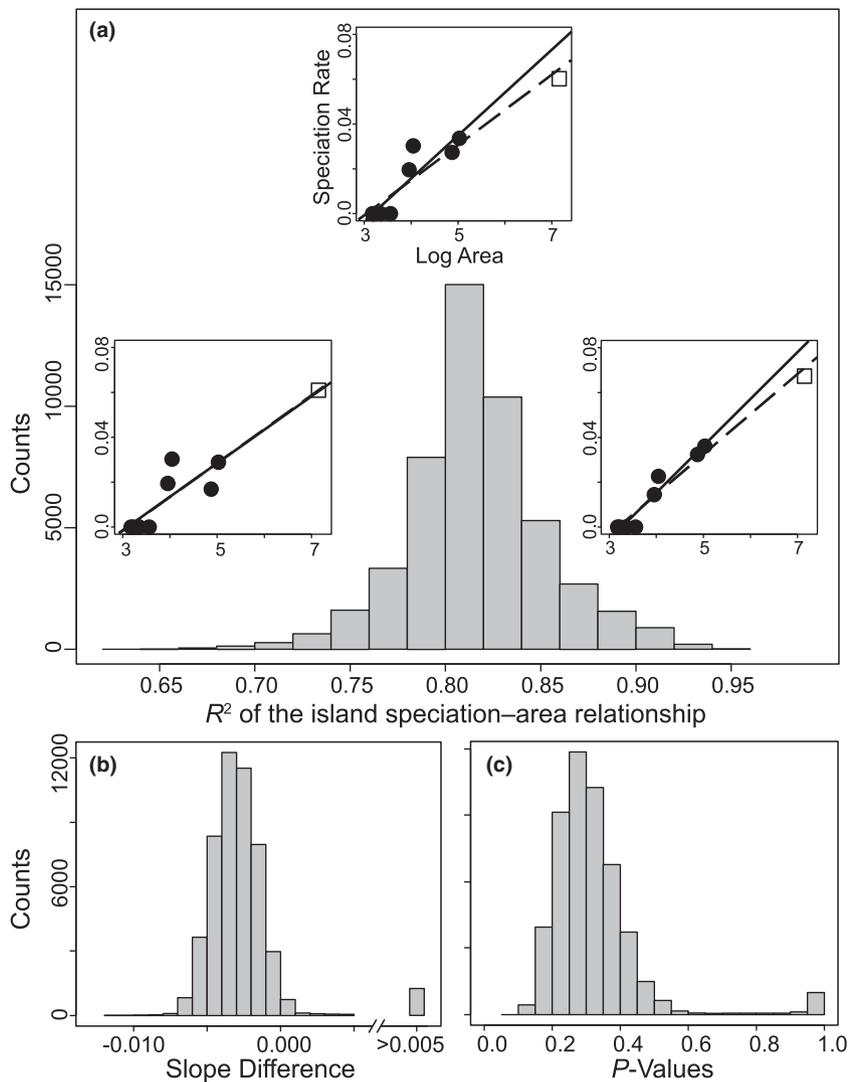
**Figure 4** *Anolis* species richness on Caribbean islands and Neotropical mainland areas versus predicted richness based on the mainland climate–richness relationship. Mainland areas are depicted by grey circles, islands without *in situ* speciation by the black circles and islands where *in situ* speciation has occurred by black diamonds. The dashed line is fitted to the island data and has a slope and intercept not differentiable from one and zero, respectively. Islands without *in situ* speciation were, on average, less species rich than mainland areas with similar climates (simultaneous autoregression,  $n = 910$ ,  $P < 0.001$ ), while islands with *in situ* speciation contained more species than similar mainland areas (simultaneous autoregression,  $n = 104$ ,  $P < 0.001$ ).

with island area (Figs 5 & 6), as found by Losos & Schluter (2000). Assuming no extinction, all slopes were positive and significant at  $\alpha = 0.05$ ;  $R^2$  values ranged from 0.64 to 0.95 (Fig. 5). Results were similar for high extinction: all slopes were again positive and statistically significant;  $R^2$  values ranged from 0.61 to 0.98 (Fig. 6).

In all 50,000 reconstructions, speciation rate was higher on the mainland than on any of the islands when area was ignored (for examples see Figs 5 & 6). However, assuming no extinction, the mainland speciation rate almost always fell within the 95% prediction interval of the island speciation–area relationship. In 44 cases (< 0.1% of 50,000 reconstructions) the mainland speciation rate was significantly lower than predicted, and in 1156 cases (2.3%) the mainland speciation rate was significantly greater than predicted. These differences may simply be due to chance (5% of the mainland rates would be expected to be outside the island prediction interval by chance alone).

Extrapolation far outside the range of the island data led to very wide 95% prediction intervals for the mainland speciation rate. Therefore, we also compared the slopes of the island regression and a regression including the mainland datum. In more than 98% of cases, the slopes did not differ; in the other 1.9% the mainland inclusive slope was greater than the island slope (Fig. 5).

Assuming a high relative extinction rate resulted in the majority of mainland speciation rates being greater than the



**Figure 5** *Anolis* speciation–area relationships for Caribbean islands and Neotropical mainlands assuming no extinction. (a)  $R^2$  values of the island speciation–area relationship (closed circles, solid lines) for 50,000 reconstructions. Insets show exemplars from the tails and median of the distribution. Axes are the same for all insets. The open square is the mainland value and the dashed lines are for the mainland-inclusive relationship. (b) Difference in slopes between the island-only and mainland-inclusive relationships. Negative values indicate a shallower slope for the latter. Note the break in the x-axis. These extreme values arose in rare cases when stochastic character mapping inferred a very recent back colonization from a small offshore island, which produced high estimates for the diversification rate in this recent mainland clade. (c)  $P$ -values (two-sided tests) for slope differences depicted in (b).  $P$ -values  $> 0.5$  represent cases where the mainland-inclusive slope was steeper than the island-only slope. No units are given for speciation rates as the Nicholson *et al.* (2005) tree was arbitrarily scaled.

95% prediction interval of the island relationship (62%). This number of relationships outside the 95% prediction interval is unlikely to have arisen due to chance. In 20% of cases, the slope of the speciation–area relationship including both island and mainland data was significantly greater than the island-only slopes. Thus, if extinction rate has been high, the mainland speciation rate may be greater than predicted by the island speciation–area relationship, although the evidence is not especially strong.

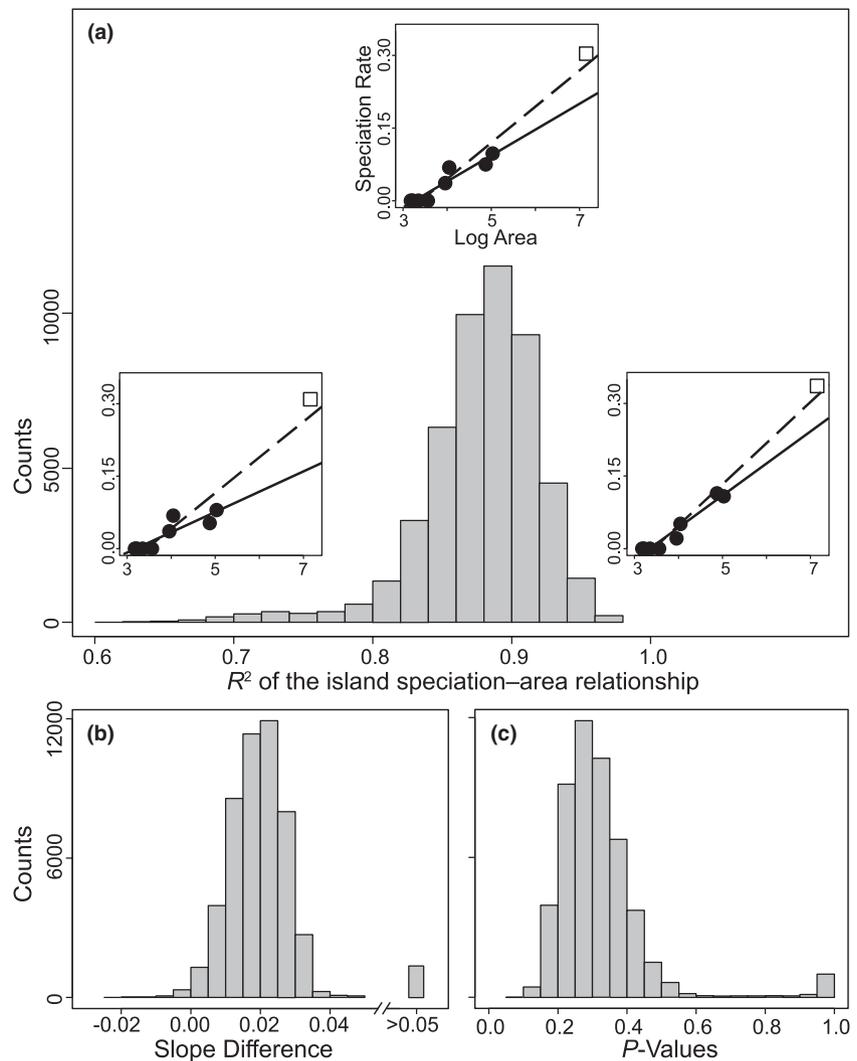
## DISCUSSION

### Speciation and island–mainland richness differences

*In situ* speciation of *Anolis* lizards on Caribbean islands has fundamentally altered the relationship between island and mainland species diversity. Island biogeographers have long suggested that islands have fewer species than similar mainland areas (MacArthur & Wilson, 1967; Carlquist, 1974; Lack, 1976; Rosenzweig, 1995). However, classic theory (e.g. MacArthur & Wilson, 1967) and subsequent work have focused predomi-

nantly on colonization and extinction as drivers of species richness on islands, with less emphasis placed on *in situ* speciation (Heaney, 2000, 2007). Here, we document that evolutionary radiation within islands can actually lead to elevated richness relative to mainlands. We found that the Greater Antilles, whose anole faunas have arisen almost exclusively from *in situ* speciation (reviewed in Losos, 2009), harbour more species of *Anolis* than similarly sized mainland areas. Furthermore, this result was not due to climatic differences between islands and the mainland; islands with *in situ* speciation have more species than predicted by the mainland climate–richness relationship, especially Cuba and Hispaniola, where *in situ* speciation has been most prevalent (Losos & Schluter, 2000).

We found a similar, although not statistically significant, result when the entire mainland was considered, rather than island-sized subregions. Although total mainland diversity was within the 95% prediction interval of the island SAR, meaning we cannot unequivocally reject the null hypothesis that island and mainland richness do not differ after accounting for area, we suspect this is due primarily to low statistical power. To



**Figure 6** *Anolis* speciation–area relationships for Caribbean islands and Neotropical mainlands assuming a high relative extinction rate ( $\epsilon = 0.90$ ). (a)  $R^2$  values of the island speciation–area relationship (closed circles, solid lines) for 50,000 reconstructions. Insets show exemplars from the tails and median of the distribution. Axes are the same for all insets. The open square is the mainland value and the dashed lines are for the mainland inclusive relationship. (b) Difference in slopes between the island-only and mainland-inclusive relationships. Negative values indicate a shallower slope for the latter. Note the break in the  $x$ -axis. (c)  $P$ -values (two-sided tests) for slope differences depicted in (b).  $P$ -values  $> 0.5$  represent cases where the mainland-inclusive slope was steeper than the island-only slope. No units are given for speciation rates as the Nicholson *et al.* (2005) tree was arbitrarily scaled.

match the richness predicted by the island SAR, thousands of species would have to be added to the mainland fauna. Many new *Anolis* species have been described in recent years, almost all of which have been mainland species, and there are probably still many undiscovered or undescribed mainland species. However, it is highly unlikely that low mainland diversity (relative to the Greater Antilles and after accounting for geographical area) is an artefact of the presence of many undescribed mainland species. For mainland richness to reach the level predicted by the island SAR, more than 2000 new species would have to be described, an almost inconceivable number considering there are fewer than 6000 extant lizard species known world-wide. Thus, given that the island SAR over-predicts mainland richness by more than an order of magnitude, we are reasonably confident in concluding that the mainland *Anolis* fauna is depauperate relative to island faunas assembled by *in situ* speciation.

The role of *in situ* speciation in generating exceptionally rich island faunas is strengthened by examining islands on which it has not occurred. If such islands also demonstrated elevated *Anolis* richness, then the greater richness of island anole faunas clearly could not be attributed to a speciation effect. However,

the Caribbean's small islands host fewer species of anoles than similar mainland areas, as predicted when colonization is the primary source of island species (MacArthur & Wilson, 1967). Also, although not significantly different, the slope estimate of the SAR on small islands was slightly steeper than the mainland SAR, as expected for islands (Rosenzweig, 1995).

Why might evolutionarily assembled islands have higher species diversity than mainlands? One possible explanation is the lack of species from other, potentially competing, taxonomic groups. Ecological divergence in Greater Antillean anoles has been facilitated by a history of ecological opportunity in (once) depauperate environments (Losos, 2010; Mahler *et al.*, 2010). However, while anoles are far and away the most diverse group of vertebrate diurnal insectivores on the islands (Losos, 2009), the mainland contains many other diverse clades of insectivorous lizards, as well as diverse clades of tree frogs, birds and other insectivores. Species from these other clades could pre-empt niche space filled by anoles on islands, leading to reduced diversity on the mainland.

Nonetheless, this explanation is not compelling, for several reasons. First, the ecological and morphological variety of mainland anoles is comparable to that of island anoles

(Velasco & Herrel, 2007; Pinto *et al.*, 2008; Losos, 2009). Second, community richness of anoles is not obviously larger on the islands (Losos, 2009). Moreover, many insectivorous mainland taxa – particularly lizards and frogs – generally differ from anoles either in their habitat use (lizards) or their activity time (frogs; Losos, 2009). Hence, it is not obvious that mainland anole diversification has been inhibited by the presence of competing mainland taxa. More work is clearly necessary to disentangle how differences in the diversity of potentially competing clades interact with ecological opportunity and environmental variation to influence the assembly and diversity of island and mainland faunas.

### Speciation rates on islands and mainlands

Larger areas are expected to have higher speciation rates by providing more opportunities for geographical isolation (MacArthur & Wilson, 1967; Rosenzweig, 1995; Losos & Schluter, 2000). Assuming a constant rate of diversification through time (a major assumption – see below), our results are consistent with this expectation. Speciation rate varied with area in a relatively consistent manner, especially if extinction was assumed to be negligible. Alternatively, when extinction was assumed to be very high (90% of the speciation rate), mainland speciation was faster than predicted by the island speciation–area relationship. However, when the relative extinction was assumed to be slightly lower ( $\epsilon = 0.8$ ), the mainland speciation rate did not differ from the island prediction in > 90% of cases (based on a random subset of 5000 reconstructions; 9% of mainland rates were greater than the island-based 95% prediction interval, and incorporating the mainland rate in a regression with area only reduced the slope in 3% of cases). Thus, even under moderately high extinction, speciation varies in a regular way with area on both islands and mainlands. Unfortunately, given the incompleteness of the mainland anole phylogeny, we could not estimate extinction rates, although even with complete sampling, such estimates can be unreliable (Rabosky, 2010).

Kisel & Barraclough (2010) have recently shown that the prevalence of *in situ* speciation on islands depends not only on the opportunities for geographical isolation afforded by large landmasses, but also on the strength of gene flow among populations. Speciation modes have been little studied in island anoles, with even less attention given to mainland species. However, even amongst island species, there is little evidence for non-allopatric speciation (Losos, 2009). Assuming allopatric speciation is dominant [as it often is (Barraclough & Vogler, 2000; Phillimore *et al.*, 2008), but see Bolnick & Fitzpatrick (2007) and Losos & Glor (2003) for limitations regarding the methods used for these inferences] and gene flow is similar among mainland and island species, then we would expect diversification rate to scale similarly with area. Alternatively, if there is weaker gene flow among mainland populations then we would expect higher than island-predicted speciation rates on the mainland, as might be the case under our extremely high extinction scenario – although the evidence for this significantly higher rate is not strong.

### Carrying capacity and inferences of island–mainland differences

Inferences of the processes underlying the patterns we have identified depend on whether island and mainland richness have reached equilibrium (carrying capacity). In general, islands do not appear to be consistently at carrying capacity (Schoener, 2010) and recent theory suggests that richness equilibria will not be constant through evolutionary and geological time (Heaney, 2007; Whittaker *et al.*, 2008). From a clade, rather than an island, perspective, evidence for carrying capacities is mixed; some studies have found density-dependent reductions in diversification rate (Phillimore & Price, 2008; Rabosky & Lovette, 2008; Rabosky, 2009b) while others have not (Venditti *et al.*, 2010). Given the uncertainty in whether island and mainland faunas are consistently at carrying capacity, we discuss three possible scenarios below.

If island and mainland anole faunas have reached carrying capacity, then, by definition, the elevated richness on islands with *in situ* speciation will persist through time (barring substantial changes to equilibria). However, when diversification rates vary through time, and especially when a clade has reached carrying capacity, estimates of diversification based on clade ages and extant diversity are unreliable (Rabosky, 2009c). Under this scenario, diversification rates could appear to increase with area because smaller islands would reach carrying capacity before larger islands, leading to an underestimation of the diversification rate on small islands (Rabosky, 2009c; Rabosky & Glor, 2010). However, such a scenario would not change our conclusion that *in situ* speciation results in elevated island richness relative to similar mainland areas.

If neither islands nor mainlands have reached carrying capacity, then our estimates of speciation rate probably represent a consistent effect of geographical area on lineage diversification, especially if extinction is low relative to speciation rate, which seems likely if clades are not close to carrying capacity. If faunas are below carrying capacity, then mainland richness is probably limited, at least partially, by the timing of the relatively recent mainland colonization by the M2 clade (Nicholson *et al.*, 2005), i.e. a time for speciation effect (Stephens & Wiens, 2003). However, this explanation cannot entirely account for low mainland richness. The M1 clade has had substantial time to speciate, yet mainland richness, especially in South America where M1 species are predominantly found, is still low.

A third possibility is that the island faunas have reached carrying capacity while the mainland has not. If this is the case, then the apparent high mainland speciation rate could be due to downward-biased estimates of island rates. Such a scenario would again suggest that mainland richness is low, at least in part, because of a time for speciation effect. However, whether the mainland carrying capacity is lower or higher than the value predicted from the island relationship is unknown. Nevertheless, although we cannot be certain whether mainland richness will surpass island richness in the future, we can still conclude that island faunas assembled by *in situ* speciation are less depauperate relative to mainland areas than are islands dominated by colonization.

## CONCLUSIONS

The past four decades of research in island biogeography have predominantly focused on how immigration and extinction influence island species richness. However, some colonizing lineages have successfully radiated in island environments, resulting in faunas that are assembled predominantly by *in situ* speciation rather than by colonization (Funk & Wagner, 1995; Heaney, 2000; Losos & Schluter, 2000; Mendelson & Shaw, 2005; Parent & Crespi, 2006; Leigh *et al.*, 2007; Losos & Parent, 2010). We have shown that for *Anolis* lizards, such evolutionary assembly results in islands with more species than similarly sized mainland areas, even after controlling for climatic differences.

How general may this result be? Kalmar & Currie (2007) found no statistical difference between island and mainland land-bird diversity once area, climate and isolation were considered. However, birds have speciated *in situ* on only a few very large islands (Diamond, 1977; Coyne & Price, 2000; Kisel & Barraclough, 2010), and thus the lack of a statistical signature of elevated island richness could be due to a paucity of evolutionarily assembled island faunas. For other lizard taxa, numerous genera inhabit both islands and mainlands, some of which contain more island than mainland species and some that do not. Similarly, *in situ* diversification of lizards has occurred on some islands but not others (Kisel & Barraclough, 2010). It is currently unknown whether the non-anole lizard taxa with more island than mainland species are also those that have diversified on individual islands. However, when considering such comparisons, it must be remembered that more island than mainland species within a genus (or vice versa) does not necessarily imply that any individual islands have greater diversity than mainland areas once climate and area have been considered.

Our results highlight the importance of considering how equilibrium and non-equilibrium dynamics can affect conclusions regarding richness comparisons among geographical domains. Further integration of how and whether lineage diversification, morphological evolution and abiotic and biotic interactions differentially influence island and mainland faunas and their ability to reach carrying capacity (if there is such a thing), will undoubtedly further our understanding not only of island environments but of mainland ones as well.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** HerpNet and Global Biodiversity Information Facility (GBIF) providers.

**Appendix S2** References for additional locality sources.

**Figure S1** Range-construction procedure.

**Figure S2** Map of mainland subregions.

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