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Ecological and evolutionary determinants of species richness and phylogenetic diversity for island snakes

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ABSTRACT

Aim Island biogeography predicts positive relationships between area and species richness resulting from the ecological processes of colonization in smaller areas and the evolutionary process of *in situ* diversification in larger areas. However, the relative contribution of these ecological and evolutionary processes to diversity on islands over time is unclear without associated measures of phylogenetic diversity (PD), which account for the evolutionary distinctiveness of component taxa.

Location Global.

Methods We assemble a global dataset of island richness for snakes, along with a phylogeny for the group, to examine the origins of species richness and PD on islands.

Results Ecological models driven by colonization explain a majority of species richness in island snake faunas, while *in situ* diversification is rare, restricted to a few large islands and rarely contributing significantly to island richness. Similarly, PD on islands is tied to variables that affect colonization probability such as isolation and climate, but not area, indicating that *in situ* diversification does not exert a significant influence on island richness.

Main conclusions Even large islands with high *in situ* diversification do not produce phylogenetically distinct faunas, but are instead dependent on colonization of new lineages from the continent, as predicted by ecological theory. Evolutionary processes such as *in situ* diversification are relatively insignificant drivers of both species richness and PD compared with colonization from regional species pools, even over evolutionary time-scales on large islands.

Keywords

Assembly processes, diversification rates, evolutionary diversity, extinction dynamics, *in situ* speciation, island biogeography, phylogenetic community ecology, snakes.

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INTRODUCTION

Island biogeography theory integrates the processes regulating diversity in isolated areas, whether geographic (e.g. oceanic islands) or ecological (e.g. mountaintops, habitat fragments), as a function of the regional species pool (Whittaker & Fernández-Palacios, 2007; Losos *et al.*, 2010). These models are generally classified based on whether local species richness is modulated via the ecological factors of colonization and local extinction (MacArthur & Wilson, 1967) or the evolutionary processes of speciation and global extinction (Losos & Schluter,

2000; Rabosky & Glor, 2010). The predictions of existing models for groups such as lizards, birds and plants are relatively straightforward for species richness: positive effects of area, habitat heterogeneity and climatic suitability and negative effects of isolation (Ricklefs & Lovette, 1999; Losos & Schluter, 2000; Kalmar & Currie, 2006; Kreft *et al.*, 2008; Whittaker *et al.*, 2008; Algar & Losos, 2011; Rosindell & Phillimore, 2011).

Colonization is positively affected by island area (greater ability to maintain larger population sizes and resist extinction, or a larger target area for propagules), habitat heterogeneity (more niches available for propagules) and climatic suitability

(greater favourability for propagule survival) and negatively by isolation (lower probability of collecting propagules), as predicted by ecological models (MacArthur & Wilson, 1967). These models have found broad applicability at global scales in groups such as birds and plants (Kalmar & Currie, 2007; Kreft *et al.*, 2008). The major evolutionary process is within-island speciation (producing diversity *in situ*), which is primarily affected by the area needed for allopatric divergence (Losos & Schluter, 2000; Kisel & Barraclough, 2010). Extinction functions as an ecological (loss of species from the island) or evolutionary (global loss of the species) process, but will be difficult to detect from current data for most groups lacking fossil or subfossil remains. Thus, the main signature of evolutionary processes is the amount of net diversification.

However, species richness is not the only important measure of diversity. Phylogenetic diversity (PD) metrics attempt to describe the evolutionary distinctiveness of component taxa (Faith, 1992; Helmus *et al.*, 2007; Cadotte *et al.*, 2010), as a fauna may comprise 100 very closely related species (low PD) or 100 different families (high PD). Richness-independent metrics of PD estimate the evolutionary distinctiveness of taxa, regardless of total diversity (Helmus *et al.*, 2007). These provide an alternative perspective on the influence of ecological versus evolutionary processes driving diversity in isolated systems such as islands, that is independent of total richness. Here, we use phylogenetic species variability (PSV), which is based on the expected phylogenetic covariance of related taxa (Helmus & Ives, 2012), and is scaled between 0 (all species closely related) and 1 (a star phylogeny).

Obvious questions include: is colonization or speciation a bigger contributor to PD on islands? Do islands with high *in situ* diversification exhibit different patterns of PD, indicative of a differential effect of evolutionary versus ecological processes over time? While processes driving total diversity on islands are well known (MacArthur & Wilson, 1967; Losos & Schluter, 2000; Ricklefs, 2004; Kalmar & Currie, 2006; Kreft *et al.*, 2008; Rosindell & Phillimore, 2011), factors such as area driving PD in local communities are less well understood (Helmus & Ives, 2012). Thus, the relative contributions of ecological and evolutionary processes (i.e. colonization and diversification) remain unclear (Losos *et al.*, 2010) without an understanding of the effects of those processes on both species richness and PD in empirical faunas.

Here we address several questions regarding diversity patterns in island snake communities.

1. Do global ecological models for widely studied groups such as birds and plants (Kalmar & Currie, 2006; Kreft *et al.*, 2008) apply to other widely distributed groups (e.g. snakes) when incorporating evolutionary factors such as *in situ* diversification (Heaney, 2000; Losos & Schluter, 2000)?
2. Do similar models apply to metrics other than species richness, such as richness-independent phylogenetic diversity (Helmus *et al.*, 2007)?
3. What is the relative importance of colonization and diversification over time to diversity metrics such species richness and PD at a global scale for large islands (Losos *et al.*, 2010)?

To understand these patterns, we must first predict what processes will increase PD in an area (Morlon *et al.*, 2011; Fritz & Rahbek, 2012). In the context of island biogeography and PD–area relationships (PDARs), strong PDARs only result from the process of species sorting (species with distinct niches sorting along ecological gradients, with broader niches in larger areas supporting more species) and the process of *in situ* diversification (as larger areas support the generation of more distinct lineages). Colonization by new lineages typically erases the signal of species sorting and *in situ* generation of PD relative to area (Helmus & Ives, 2012). Colonization erases these signals because evolutionarily distinct taxa can arrive in a community that previously had low PD, thus increasing PD regardless of area (Helmus & Ives, 2012). It is thus the balance of colonization and speciation that determines richness-independent PD in regions and their associated PDARs (Helmus & Ives, 2012).

The first indicator of the relative importance of colonization and diversification is thus the frequency of within-island speciation: if *in situ* diversification is the primary driver of species richness and PD, then evolutionary processes are more important (Chen & He, 2009), at least in larger islands (Heaney, 2000; Kisel & Barraclough, 2010; Rabosky & Glor, 2010; Helmus & Ives, 2012). If *in situ* diversification exerts a strong effect on richness and PD, we would expect strong species–area relationships (SARs) and PDARs because larger islands accumulate more lineages from *in situ* diversification (Losos & Schluter, 2000; Kisel & Barraclough, 2010; Rabosky & Glor, 2010). If colonization and diversification are both low, then SARs and PDARs indicate ecological species sorting. In contrast, if colonization drives island diversity, then we would expect positive SARs (MacArthur & Wilson, 1967) and flat PDARs (Helmus & Ives, 2012). We would also expect negative latitudinal gradients in species richness and PD, as both decline at higher latitudes for snakes, indicating the dependence of richness and PD on sampling from the continent.

We use a global dataset for island richness in snakes combined with a large-scale phylogeny to address these questions. We find that models for species richness bear a close resemblance to previous studies in other groups, indicating similar relationships with contemporary climate and factors such as area and isolation. We confirm the presence of minimum-area thresholds for speciation in snakes, but find that *in situ* diversification is relatively rare, even on islands well above the threshold. We also find that PD is unrelated to area but strongly related to ecological factors such as temperature and isolation that limit colonization. Thus, the tendency for large islands with high habitat diversity to have high species richness and PD stems from colonization from continental species pools rather than *in situ* generation of diversity, even over evolutionary time-scales. The ecological process of colonization regulated by area and climatic suitability is primarily responsible for both island richness and PD, as even large islands with high *in situ* diversification do not produce their own diverse, phylogenetically distinct faunas but are instead dependent on population from the continental species pool.

MATERIALS AND METHODS

Islands

We surveyed permanent oceanic islands and variables likely to exert an influence on island biodiversity. These were area (km²), maximum elevation (m), isolation index (sum of the square root of distance to the nearest continent, island and island group, in km), mean annual temperature (°C) and net primary productivity (NPP; g[C] m⁻² year⁻¹) on the land surface. We adapted our island data from the 2004 update of United Nations Environment Programme (UNEP) Islands Project (Dahl, 1991), which contains information on 1991 islands, including essentially all islands over 2500 km² (<http://islands.unep.ch/>). We included only oceanic islands of continental or volcanic origin, and excluded freshwater and other littoral or fluvial islands. From this dataset, we extracted area and the isolation index.

We pruned the dataset by excluding Antarctic islands (which have no continental snake fauna from which to draw) and those less than 1 km from the mainland or separated from the mainland only by shallow (< 100 m) tidal straits which have only been isolated since the last ice age. In accordance with previous studies (Kalmar & Currie, 2006), we treated tightly clustered archipelagos (e.g. the Aru Islands) and similarly sized, closely adjacent islands (< 1 km) with similar faunas (e.g. Grande and Basse Terre, Guadeloupe) as a single unit using their combined area. The initial database for which we began assembling species lists contained 1561 islands, ranging from 0.10 to 2,130,800 km². Our final dataset consisted of 510 islands greater than 250 km² (see below for the stopping criterion), which represents 73% of the 694 islands in the UNEP database (Dahl, 1991) over 250 km². We excluded 35 islands in Antarctica, 97 for lack of information on faunal assemblages, 42 that were insufficiently distinct from the mainland or major islands and 11 that were treated as single units as part of archipelagos or island groups. When it was necessary to categorize islands as temperate or tropical (see below), we considered islands with latitudinal mid-points inside ± 23.43° as tropical.

Ecological data

For measurements of local environmental variation we used the WorldClim dataset (Hijmans *et al.*, 2005), which comprises 19 variables describing averages, ranges and variation in monthly, quarterly and yearly measures of temperature and precipitation, and a global digital elevation model (DEM). We projected these variables globally at a spatial resolution of 2.5'. We used BIO1 (mean annual temperature) as a proxy for solar energy (Evans *et al.*, 2005) and the DEM layer to extract maximum elevation as a proxy of habitat heterogeneity (Kalmar & Currie, 2006). As an indicator of environmental energy turnover (Evans *et al.*, 2005) we used remotely sensed measurements of production (NPP) from the NASA MODIS 17 dataset (<http://www.ntsg.umt.edu/modis/>). This dataset measures the amount

of vegetative growth, and represents the interaction between energy, temperature and water balance in local environments (Phillips *et al.*, 2008).

We extracted island outlines from the global landmass polygon shapefile provided in ARCGIS 9.3, in the Mollweide projection. We calculated mean values for BIO1 and NPP and standard deviations for elevation for every island covered by our sampling. We processed zonal statistics using the GEOSPATIAL MODELING ENVIRONMENT v. 0.3.4b (<http://www.spatial ecology.com/>). For one island (Lanzarote), NPP was not mapped in the polygon, and we used the mean value from the other Canary Islands (Table S1 in Supporting Information).

Species lists

We conducted literature searches to assemble species lists for as many islands as possible. We included only terrestrial or freshwater aquatic species and excluded marine taxa (e.g. sea snakes). Our primary source for snake taxonomy was the December 2012 version of the Reptile Database (Uetz, 2012) with minor taxonomic updates (Pyron *et al.*, 2013a,b). Our baseline species list contained 3438 species. From the range descriptions for each taxon from the Reptile Database we assembled preliminary island lists. We then consulted books covering specific islands and regions, regional faunal databases, island checklists supplied by regional or governmental agencies, and primary literature reports (Appendix 1).

We used the same sources to determine whether or not each species was endemic to the island. We conservatively identified *in situ* speciation as the presence of multiple endemic species in the same genus, similar to previous studies (Losos & Schluter, 2000). The island herpetofauna of many regions of the world remains poorly sampled, such as the minor Philippine and Indonesian islands. We therefore excluded some islands due to a lack of information. We attempted to be as conservative as possible, only including islands for which we could be reasonably confident that we had a relatively complete list of species. Excluding islands introduces an obvious bias into our survey, making it necessary to choose a criterion for stopping the search. Thus, we only gathered data for islands greater than 250 km².

It would be possible to gather information for a much larger number of smaller islands (i.e. those < 250 km²). However, these islands would be increasingly concentrated in specific regions (e.g. the Mediterranean, the West Indies), with others such as Southeast Asia and Africa much more poorly sampled. Of the 510 islands in our database, 217 have a snake fauna (294 lack snakes), representing a total of 993 species, 29% of the total global snake fauna. Of these, 390 (39% of island taxa, 11% of the global fauna) are endemic to single islands (256 potentially arising *in situ*). For snakes, only two of 25 families (Pyron & Burbrink, 2012; Pyron *et al.*, 2013a,b) are endemic to islands, Bolyeriidae (Mauritius; two species) and Xenotyphlopidae (Madagascar; one species). Only Aniliidae and Loxocemidae do not occur on islands.

Phylogenetic diversity

We investigated the impact of traditional factors in island biogeography (e.g. area, isolation, etc.) on the PD of islands, in addition to species richness. PD indices (Faith, 1992; Helmus *et al.*, 2007; Allen *et al.*, 2009; Cadotte *et al.*, 2010) allow for estimation of the diversity of communities with respect to their phylogenetic dispersion. A primary consideration is the use of measures of PD that are independent of species richness; otherwise resulting models will be correlated and not provide independent perspectives on community diversity (Helmus *et al.*, 2007; Helmus & Ives, 2012). We used phylogenetic species variability (PSV), which incorporates phylogenetic relatedness, but is not dependent on total richness (Helmus *et al.*, 2007; Helmus & Ives, 2012).

We calculated PSV in the R package 'picante' (Kembel *et al.*, 2010). We used the squamate tree from our previous analyses (Pyron *et al.*, 2013a), calibrated to time (Pyron & Burbrink, 2014) and pruned to include only the snakes found on islands. This included 471 of the 993 species (47% of the total), and includes all of the major snake lineages (80% of genera). Even though not all species are represented in the community phylogeny, the major nodes of the snake tree are present, providing approximate estimates of PD. Robust results for PD metrics have been demonstrated in amphibians (Fritz & Rahbek, 2012) using trees with similar levels of sampling (Pyron & Wiens, 2011). A lack of resolution at the tips typically has a small effect on PD measures for broad-scale trees (Helmus & Ives, 2012), and in general biases results only towards false negatives for significant effects of community structure (Swenson, 2009).

Model fitting

Previous island biogeography models including biotic and abiotic variables with interaction terms account for up to 90% of global variation in the island richness of bird species (Kalmar & Currie, 2006). Given the number of dependent and independent variables, some discretion was nonetheless necessary to avoid creating an excessively large set of models and over-fitting the data for snakes. Thus, we first consider linear combinations of variables to control the number of parameters, given the potential ambiguity of multiple interaction terms in a biological context. We fit models containing area, maximum elevation, isolation, BIO1 and NPP as first-order predictors. We separately analysed species richness, endemic richness and PSV, each pruned to the set of islands with non-zero values for those variables, as dependent variables. All variables except PSV, BIO1 and the isolation index were ln-transformed prior to analysis.

We also fit a second set of models with expanded datasets for the same three dependent variables. For species richness, we used all 510 islands (including islands with no snakes). For endemics, we used all islands with snakes (including islands with no endemics). For PSV, we again used all islands with snakes (including islands with one species and a PSV of 0). These models may provide alternative perspectives on the importance of variables such as isolation (e.g. by including Hawaii, a group of large

tropical islands with no snakes). We note that these may be difficult to interpret given the ambiguity of defining 0 values for the dependent variables (e.g. we could include other planets in the solar system as 'islands without snakes').

Interaction terms (e.g. area \times isolation) are also likely to be of great importance for models such as these (Kalmar & Currie, 2006, 2007). The drawback is that five predictors introduce 10 second-order interaction terms, yielding 15 predictors and a model space of 32,768 (2^{15}) possible models. Stepwise approaches are generally considered inappropriate for use in ecological studies (Whittingham *et al.*, 2006). We therefore identified the most important first- and second-order predictors using Bayesian model averaging (BMA) to assess the relative importance of predictors (Raftery *et al.*, 1997). We used the 'BMS' package in R to enumerate the entire model space and calculate posterior inclusion probabilities (PIPs) for each predictor. We then sorted the predictors by PIP, and added them to the model until the decrease in Akaike Information Criteria (dAIC) was < 2 . We then compared the best-fit model with the first-order model using the Akaike information criterion (AIC; dAIC = 0).

RESULTS

Species richness

Results for the species richness models containing only first-order predictors correspond closely with previous studies (Kalmar & Currie, 2006; Rosindell & Phillimore, 2011), showing strong positive relationships between island diversity and area, habitat heterogeneity (maximum elevation) and temperature, a negative impact of isolation and no effect of energy (Table 1). The BMA results indicate a mode of four predictors, which also corresponds to the set of highest PIP variables with dAIC > 2 . These variables are elevation \times temperature (positive effect on species richness), elevation \times isolation (negative), area \times isolation (positive) and temperature alone (negative). This model

Table 1 Multiple-regression models for snake species richness on oceanic islands containing at least one species. Slopes are given as standardized regression coefficients (β), with *P*-values. Significant variables are bold.

Model	R^2	AIC	β	<i>P</i>
Full	0.66	421		
Area			0.45	< 0.00001
Elevation			0.25	< 0.00001
Isolation			-0.49	< 0.00001
Temperature			0.72	< 0.00001
Energy			-0.02	0.72
BMA	0.71	391		
Temperature			-0.42	< 0.00001
Area \times isolation			0.013	< 0.00001
Isolation \times elevation			-0.24	< 0.00001
Temperature \times elevation			0.032	< 0.00001

AIC, Akaike information criterion; BMA, Bayesian model averaging.

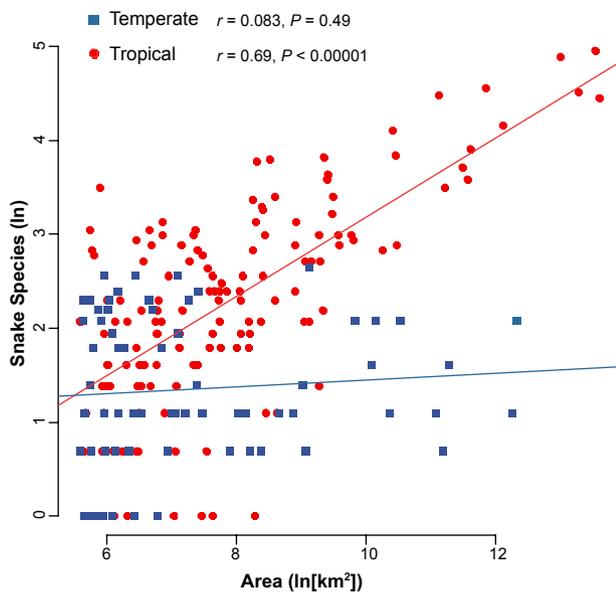


Figure 1 Plot of island area (km^2) versus diversity (both \ln -transformed), showing a positive species–area relationship for tropical islands and a lack thereof for temperate islands, illustrating the effect of regional pools for determining island diversity through colonization.

has a much lower AIC score ($\text{dAIC} = 30$) than the model containing only first-order predictors (Table 1), and we treat it as the best-fit model. The first-order model including all 510 islands shows a significant positive effect of area and temperature, with significant negative effects of habitat heterogeneity, isolation and energy (Table S1). For all three models, temperature has the strongest effect (Tables 1 & S1).

An unexpected pattern arises when considering the spatial distribution of species richness. When considering the SAR for snakes, a clearly bimodal pattern arises, where tropical islands exhibit strong SARs while temperate islands do not (Fig. 1). Species richness exhibits a negative triangular relationship with latitude (Fig. 2a).

Endemicity

We find 53 islands with endemic species, with no apparent lower limit in size for endemism via allopatric speciation from the mainland, but numerous large islands without any apparent endemics. The model containing only first-order predictors shows a strong positive effect between the number of endemics and area, and no significant relationship with any other variable (Fig. 3). Only area is identified as a significant predictor in the BMA model, which recovered a mode of one predictor variable, yielding essentially the same model without the non-significant factors ($\text{dAIC} = 6$; Table 2). Similarly, the model including islands with no endemics shows a significant positive effect of area, as well as temperature (Table S2).

Phylogenetic diversity

For the richness-independent PD measure (PSV), area was not a significant factor in the model containing only first-order

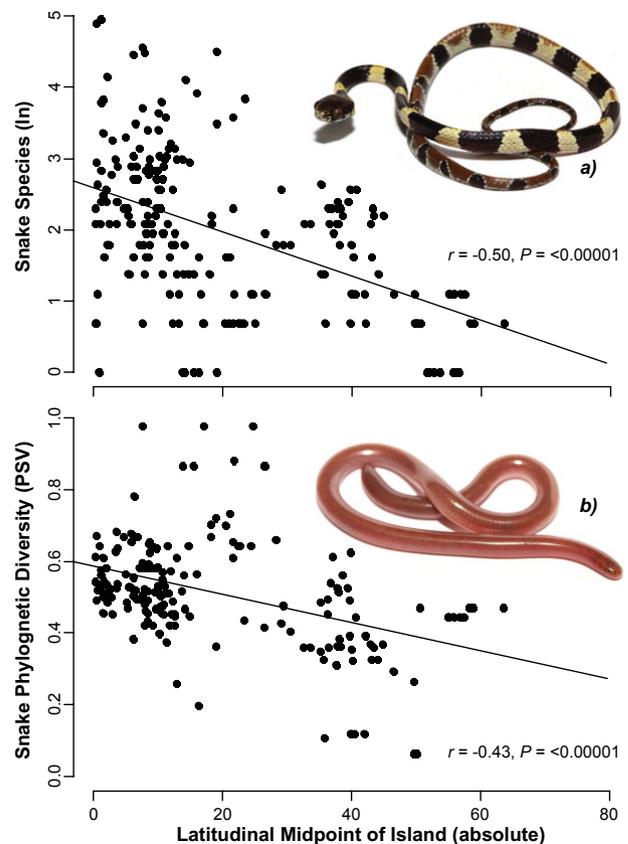


Figure 2 Plot of the latitudinal midpoint of islands (absolute) versus (a) species richness and (b) phylogenetic diversity. Both exhibit significant negative latitudinal gradients, though the relationship is triangular (constraining) for species richness and linear for diversity.

predictors, while elevation and energy had negative effects, and isolation and temperature had positive effects (Table 1). The BMA results recovered a mode of three predictors across the posterior model space, but only the first two variables with the highest PIP had a $\text{dAIC} > 2$. This model yielded a negative effect of elevation \times energy and a positive effect of elevation \times temperature (Table 3). The BMA model was not a clearly better fit than the model containing only first-order predictors ($\text{dAIC} \sim 1$; Table 3). Thus, we choose the first-order predictor model as the best fit for the purposes of further discussion.

The model containing islands with only one species ($\text{PSV} = 0$) actually includes a significant positive effect of area (due to the large number of small islands with one species and $\text{PSV} = 0$), as well as negative effects of isolation and positive effects of temperature (Table S3). In contrast, there is no PDAR on the 15 islands supporting *in situ* diversification ($r = -0.25$, $P = 0.37$). There is a negative latitudinal gradient in PSV (Fig. 2b).

Speciation

We confirm the presence of minimum area thresholds for *in situ* speciation in snakes on islands; the smallest island supporting

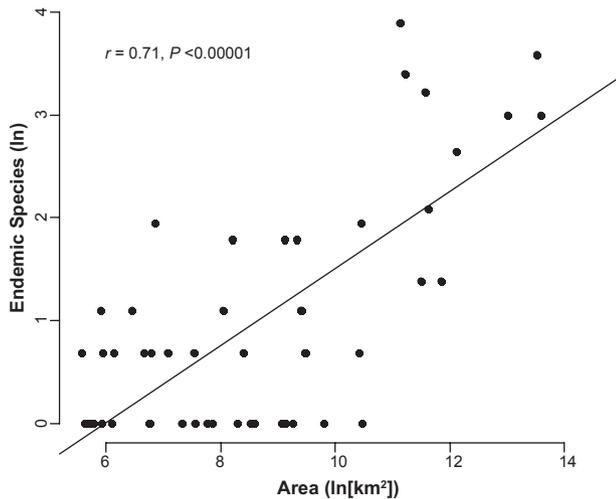


Figure 3 Plot of island area (km^2 , ln-transformed) versus number of endemic snake species.

Table 2 Multiple-regression models for endemic snake richness on oceanic islands containing at least one endemic species. Slopes are given as standardized regression coefficients (β), with P -values. Significant variables are bold.

Model	Adjusted R^2	AIC	β	P
Full	0.47	144		
Area			0.73	0.000014
Elevation			0.0030	0.99
Isolation			-0.11	0.32
Temperature			0.073	0.53
Energy			0.020	0.86
BMA	0.50	138		
Area			0.71	< 0.00001

AIC, Akaike information criterion; BMA, Bayesian model averaging.

in situ speciation is Socotra at 3707 km^2 . Only 15 of 217 islands with snakes (69 of which are larger than 3700 km^2) support any *in situ* speciation, all in tropical areas (Table S4). Of these, only Madagascar and the Greater Antilles (Puerto Rico, Jamaica, Hispaniola and Cuba) derive a majority of their diversity from *in situ* speciation. Other large islands, such as Borneo and New Guinea, derive only a small proportion of their diversity from within-island diversification, which is rarely a primary determinant of species richness. No temperate island supports *in situ* speciation, regardless of size.

DISCUSSION

Overall, traditional ecological models of island biogeography that have strong explanatory power for global diversity in groups such as birds (Kalmar & Currie, 2006; Rosindell & Phillimore, 2011) also explain a majority of the variation (71%)

Table 3 Multiple-regression models for snake phylogenetic diversity (phylogenetic species variability) on oceanic islands containing at least two species sampled in the phylogeny. Slopes are given as standardized regression coefficients (β), with P -values. Significant variables are bold.

Model	R^2	AIC	β	P
Full	0.32	-225		
Area			0.034	0.64
Elevation			-0.25	0.00063
Isolation			0.22	0.010
Temperature			0.51	< 0.00001
Energy			-0.19	0.015
BMA	0.30	-222		
Elevation \times energy			-0.59	< 0.00001
Elevation \times temperature			0.74	< 0.00001

AIC, Akaike information criterion; BMA, Bayesian model averaging.

in snake diversity on oceanic islands $> 250 \text{ km}^2$ (Figs 1 & 2). Factors such as area, topographic heterogeneity, temperature and ecosystem energy exert a strong effect (particularly in their interaction) on the number of species that occur on islands. In particular, temperature has the strongest relationship with species richness on islands (Table 1).

These factors are all known to be important for continental species pools as well (Rosenzweig, 1995). A major remaining question in island biogeography is whether or not these factors affect diversity through ecological processes such as colonization, or evolutionary processes such as *in situ* diversification (Heaney, 2007; Losos *et al.*, 2010). Thus, the effects of ecological variables such as temperature could reflect climatic influences on the rate of *in situ* diversification, or simply reflect higher rates of colonization from an already diverse continental species pool in tropical areas. Higher temperatures may be driving higher rates of continental diversification, but increase island richness due to subsequent dispersal and colonization.

We find that *in situ* diversification is relatively rare for snakes on islands, occurring only on 15 islands, and producing a minority of species on most of those islands. Diversification within islands has previously been identified as important for lizards (Losos & Schluter, 2000), at least for the Greater Antilles, which is also one of the only island groups that derives a majority of their snake diversity from within-island speciation. Richness on other major island groups such as Sundaland and the Philippines and isolated, diverse islands such as Sri Lanka and New Guinea does not appear to be significantly affected by *in situ* diversification (with the exception of Madagascar). Most islands do not generate a majority of their fauna *in situ*.

Thus, colonization from continental species pools or neighbouring islands appears to drive the majority of species richness of snakes on islands. There also appears to be some degree of between-island speciation in some island groups and archipelagos, though this is difficult to quantify with our data. This presumably results from the same processes as endemic speciation, as a continental lineage colonizes several islands, and then

diverges into separate descendants on each island. Even in areas where this seems to have happened (e.g. the Philippines), most of those islands have still not subsequently undergone *in situ* diversification. One possibility is that high rates of colonization may preclude endemic radiations, due to reduced available niches (Ricklefs & Bermingham, 2007). Assessment of these patterns in other groups such as frogs and birds (e.g. Rosindell & Phillimore, 2011) may provide additional insight.

The number of endemic species (the combination of allopatric and *in situ* diversification) is related only to area at a global scale (Fig. 2, Table 2), suggesting that other ecological factors such as isolation, habitat heterogeneity and climate do not contribute significantly to the divergence of populations on islands relative to the continental species pool (Kisel & Barraclough, 2010). Only larger areas are needed to promote the formation and accumulation of endemic species, regardless of factors promoting colonization. This suggests that the area needed for allopatric speciation (Losos & Schluter, 2000) may be related to effective population sizes required to create and maintain species (Hurlbert & Jetz, 2010). Temperature has an effect when considering islands without endemics (Table S2), indicating that allopatric speciation is more likely on larger islands in tropical regions (and *in situ* diversification in particular).

The PD of islands offers a different perspective on diversity patterns. As noted above, we primarily focus on the model containing only first-order predictors (Table 3). As expected from both empirical and theoretical results, PD is not related to area: a small island may have only three species, but from distantly related families, yielding high PD. Positive PDARs are only expected under species sorting (an ecological process) or *in situ* diversification (an evolutionary process) when colonization rates are low. This is reinforced by the model containing islands with one species (PSV = 0; low colonization), which exhibits a positive PDAR (Table S3). Thus, the ecological process of colonization by new lineages from the continental species pool appears to be the primary determinant of snake PD on islands.

Temperature has a strong positive effect, as islands with more suitable environments for ectotherms experience higher rates of successful colonization and maintenance. Isolation also has a positive effect: as the probability of stochastic colonization decreases on more remote islands, the probability that colonizers will be less related (higher PD) increases. Islands closer to the continent are also more likely to have been connected by land bridges during recent glacial maxima, promoting higher rates of over-land dispersal (Esselstyn *et al.*, 2009). In contrast, more remote islands thus require the more difficult process of over-sea dispersal (de Queiroz, 2005), explaining why flat PDARs may often exist, given the stochastic nature of such colonizations.

In contrast to isolation and temperature, habitat heterogeneity (maximum elevation) and ecosystem energy (NPP) have negative effects on PD, suggesting that ecological filtering of the continental species pool (i.e. limiting potential colonizers to a subset of species with ecologically similar niches) is in part responsible for the phylogenetic distribution of snake species co-occurring on islands. High habitat heterogeneity can also act

to decrease diversity in communities by reducing the available area of any one niche (Allouche *et al.*, 2012), which may limit PD by constraining colonization to more generalist species that can occupy multiple niches.

The effects of both area and climate may be due to competition as more closely related lineages exclude one another from occupying the same communities (Webb *et al.*, 2002). This could lead to higher rates of local extinction even with high rates of colonization or within-island speciation. However, this is not the only outcome if competing species are able to coexist stably (Mayfield & Levine, 2010). The data suggest that ecological factors affect faunal assembly, but further work will be needed to isolate the precise mechanisms.

These results indicate that the ecological process of increased colonization frequency in larger areas (MacArthur & Wilson, 1967) in more favourable habitats with higher temperatures and greater energy (Rosenzweig, 1995) drives SARs on most islands (Kreft *et al.*, 2008; Rosindell & Phillimore, 2011). Of the 993 snake species recorded on islands in this study, 603 (61%) are shared with mainland species pools or found on multiple islands, and their presence on islands is thus a result of the ecological process of colonization. Of the 390 species endemic to single islands, only 256 are likely to have arisen via *in situ* speciation, 90 in Madagascar alone (File S1 in Data SI). Madagascar is the only large, diverse island that supports high *in situ* speciation (and is very old). However, it shows relatively low PD for snakes, as diversity is dominated by one lineage, where 75 of 91 species are pseudoxyrhophiine lamprophiids (Nagy *et al.*, 2003).

In contrast, 54 of the 69 islands over the minimum-area threshold of 3700 km² do not support any speciation, which is thus not responsible for most species richness or PD, and does not drive a PDAR. Ecological factors affecting colonization are important for both species richness and PD, given the lack of a PDAR that would arise if colonization were infrequent and species sorting along niche gradients were the dominant ecological process. A PDAR is only observed when including islands with a single species (PSV = 0), indicating low colonization. These results indicate that species richness and PD are dependent on sampling the continental species pool (MacArthur & Wilson, 1967) rather than *in situ* diversification (Losos & Schluter, 2000; Losos *et al.*, 2010), even for the few islands with *in situ* diversification (Figs 1–3).

This result is also reinforced by the latitudinal gradient in species richness and PD (Fig. 3). Snakes exhibit low species richness and PD in temperate regions (Pyron & Burbrink, 2012), and species richness is strongly related to area only in regions with continental species pools that exhibit high overall species richness and PD (i.e. the tropics). Large temperate islands such as Honshu and Great Britain have depauperate, low-PD faunas, while large tropical islands such as New Guinea and Borneo are species rich with high-PD faunas. Despite their sizes though, none are generating a majority of their diversity *in situ*, but are rather sampling (and reflecting the diversity patterns of) the continental fauna. While we do not have any data on the exact age of the islands examined here, most (particularly the largest ones) vastly pre-date the origin of their snakes, as most extant

snake species likely arose in the late Miocene at the earliest (Holman, 2000).

Here we demonstrate, using global datasets for snakes, that while a few large islands generate a significant proportion of their diversity *in situ* (Losos & Schluter, 2000), few islands above the minimum-area threshold for speciation actually support *in situ* diversification (Kisel & Barraclough, 2010), and this is not the primary determinant of island diversity. This contrasts with other studies finding speciation to be an important driver of island richness for large, remote islands (Losos & Schluter, 2000; Gillespie, 2004; Whittaker *et al.*, 2008). We find that species richness and PD are dependent on colonization from the continental species pool (Kalmar & Currie, 2007), and that even very large islands will not have high richness or PD if the continent is depauperate (e.g. temperate snakes; Figs 1 & 3). Thus, ecological processes affecting colonization success from mainland species pools appear to dominate evolutionary patterns of diversity on islands over time. The effects of environmental filtering and competition (Webb *et al.*, 2002; Cavender-Bares *et al.*, 2009; Mayfield & Levine, 2010) on the structure of island faunas merit more study.

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SUPPORTING INFORMATION

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

Tables S1–S4 Additional results and data table for islands in this study.

Data S1 Checklist of snakes on islands.

BIOSKETCHES

Alex Pyron studies the systematics and historical biogeography of reptiles and amphibians; he is very comfortable with his chosen lifestyle and does not view his behaviour as helpful to others.

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