LETTER

Insularity and the determinants of lizard population density

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Abstract

The relative effects of resource availability and partitioning on animal population density are unresolved yet central to ecology and conservation. Species-depauperate islands offer an intriguing test case. Across 643 lizard populations from around the world, local abundances are one order of magnitude higher on islands than on mainlands, even when controlled for resource availability. On mainlands, predator and competitor richness only weakly correlate with lizard densities. On islands, sharp reductions in predator and competitor richness are the dominant drivers of lizard abundance. Our results demonstrate the dramatic effect insularity has on the interplay between biotic and abiotic control of animal abundances and the heightened sensitivity of island communities to species' losses and gains.

INTRODUCTION

Population densities are governed both by total resource availability and the partitioning of resources between species in a community (Damuth 1981, 1987; Tilman 1994). The relative importance of environmental (total resource availability) and ecological (resource partitioning) constraints in limiting population density has been widely debated (Case & Bolger 1991; Gotelli & McCabe 2002). Resource partitioning is affected by complex community assembly rules that determine the number of interacting species (Ritchie & Olff 1999). While species interactions are often found to regulate density at local scales (Schoener 1983), the most frequently demonstrated constraint on population density at broad scales is environmental resource availability (at least partially due to methodological limitations, Currie *et al.* 2004; Meehan *et al.* 2004). Models including consumer-resource theory (Tilman 1994) attempt to integrate environmental and ecological constraints on populations, but have not been empirically tested at broad spatial scales.

Islands offer an intriguing test case for disentangling environmental and ecological constraints. Because of their isolation and variation in area, islands have distinctive extinction and colonization dynamics (MacArthur & Wilson 1967). Reduced species numbers and interactions on islands alter the balance of environmental and ecological control of population dynamics in ways that only become apparent by comparison with mainland populations (Wright 1980).

The depressed number of species on small or isolated islands may lead to ecological release and increased population densities. MacArthur *et al.* (1972) termed the phenomenon density compensation. Density compensation has been demonstrated for birds (Grant 1965; Diamond 1970; MacArthur *et al.* 1972), mammals (Sara & Morand 2002), fish (Tonn 1985) and most extensively for lizards (Case 1975; Case & Bolger 1991; Rodda & Dean-Bradley 2002) in particular regions. However, its generality remains untested (Connor *et al.* 2000). Ecological release on islands offers a natural experiment for understanding the relative roles of environmental and ecological constraints in shaping animal abundances. We first assess the ubiquity of density compensation across lizard taxa and regions using 643 lizard populations from around the world. We subsequently test the hypotheses that reduced (i) predation or (ii) competition on islands (both relative to the mainland and among islands) reduces ecological constraints and increases environmental constraints on lizard densities.

METHODS

We gathered 470 measures of mainland lizard population density and 173 measures of island reptile population

density from the literature, expanding from those compiled by Rodda *et al.* (2001). The database includes 334 species and 20 families (see Appendix S1 for literature sources). Islands were defined as dispersal limited due to isolation from the mainland and with areas less than 9000 km^2. The observations were geo-referenced in BioGeoMancer (http://www.biogeomancer.org) using text descriptions of study locations. While the studies vary in methodology and quality, there is little evidence of systematic biases in density estimates between islands and mainlands (Appendix S2). Including methodological factors in the analysis did not alter our conclusions (Appendix S2). Approximately half (316 of 1643) of the observations are from studies of the entire lizard community. As most potential data biases (e.g. foraging strategy, diet, thermal physiology, morphology, sampling method) are phylogenetically conserved, accounting for phylogenetic correlation increases the robustness of the analysis.

Mass and length [snout vent length (SVL)] data were assembled from the source articles and from regional guides. We used mass estimates from Rodda *et al.* (2001, masses obtained by personal communication), which were available for the vast majority of species and accounted for the size distribution of sampled individuals. The mass estimates thus include some intraspecific variation. When mass was not available, we used a well-established relationship to convert mean lizard SVL (mm) to mass (g) (Pough 1980): $M = 3.1 \times 10^{-5} \times SVL^{2.98}$. We omitted the population densities of the largest nine island lizards (mass > 1500 g) from the analysis as low-density outliers by examining Cook's distances. The omitted species are either monitor lizards (*Varanus*) on small islands or endangered iguanas (*Cyclura*). Omitting the data did not influence our conclusion regarding the magnitude of the island effect. However, the scaling of population density with energy use on islands is steeper if the large lizards are included.

Population density (N) is expected to be approximately proportional to individuals' rate of energy use (B) and the amount of energy available to the population (P; $N \propto P/B$). We first control for rates of energy use, which have been demonstrated to constrain the abundances of mammals (Damuth 1987; Jetz *et al.* 2004), birds (Nee *et al.* 1991; Meehan *et al.* 2004), and lizards (Buckley, Rodda and Jetz, unpublished data). In ectotherms, metabolic rates scale with body mass approximately to the three-fourths and exponentially with temperature (Gillooly *et al.* 2001). Accordingly, we estimate a lizard's annual energetic use (B, kJ year^{-1}) by integrating its basal metabolic rate across hours, days and months:

$$B \propto \sum_{m=1}^{12} \sum_{h=1}^{24} M^{3/4} \, e^{-E_i/kT_{h,m}}$$

where $e^{-Ei/kT}$ is the Boltzman factor, E_i the average activation energy and k is a constant ($e^{-Ei/kT} = e^{26.68-8780/T}$ for reptiles, Gillooly *et al.* 2001). $T_{h,m}$ is the absolute temperature for hour h and month m and is calculated using the monthly mean daily temperature, the monthly mean diurnal temperature range (degrees K, data from 1961 to 1990 with 10$'$ latitude/longitude resolution, New *et al.* 2002), and a sine approximation of the temperature trend (Campbell & Norman 1998). Here, we use the metabolic cost calculation that provided the best balance of performance and complexity among a series of calculations incorporating sequentially more refined environmental temperature estimates (Buckley, Rodda and Jetz, unpublished data). We next control for the amount of available energy in the environment using minimum net primary productivity (P), which is the mean productivity of the three months with the lowest productivity according to the DOLY model (t C ha^{-1}-year^{-1}, 0.5° spatial resolution, 18-year mean, Woodward *et al.* 1995).

We next investigate potential ecological drivers of differential densities on islands. Specifically, we test the hypothesis that reduced predation or competition on islands (both relative to the mainland and among islands) reduces ecological constraints and increases environmental constraints on lizard densities. Densities of interacting species were not available. We thus use the species richness (SR) of individual taxa as proxies for predation and competition strength on lizards, the majority of which are insectivorous (Vitt & Pianka 2005). We quantify richness of potential predators and competitors using published distribution databases and range polygons. Mammal and bird richness was previously derived using single-species polygon range maps from regional guides by Ceballos *et al.* (2005) and Jetz (unpublished data), who used regional guides to distinguish insectivores (competitors) and carnivores (predators). Species richness was counted within equal area equivalents to 1° grid cells (110 × 110 km). Polygon range maps were likewise used for lizards and snakes in North America (http://www.natureserve.org). Lizard and snake range polygons were not available for other regions. For the Caribbean Islands, we used island-specific species lists available from EarthTrends (http://www.earthtrends.wri.org). Elsewhere, the best available data were species lists by WWF ecoregion (http://www.worldwildlife.org/wildfinder). We did not distinguish lizards and snakes by diet. The effects of these groups may thus be considered combined predation and competition effects, although lizards are expected to compete more strongly than they predate and snakes are expected to predate more strongly than they compete.

All data were log$_{10}$ transformed. All model effects are reported in the text with 95% confidence intervals. Several records with zero values for environmental data were omitted from regressions to enable log$_{10}$ transformation.

We added 1 to the richness of predatory birds, snakes and carnivorous mammals to enable $\log_{10}$ transformation. Akaike's information criterion (AIC) values were used to compare model goodness-of-fit (Burnham & Anderson 2002). The best model is that with the lowest AIC value.

Model residuals may be spatially non-independent. In a second step, we repeated our analyses to account for spatial autocorrelation using maximum-likelihood spatial autoregressive models (R package spdep, Bivand 2005). Longitude and latitude were used to develop neighbourhoods with threshold distances of 400, 800 and 1500 km. Threshold distances were selected by examining correlograms. Neighbours were weighted *a priori* using row standardization, such that the weights of all neighbours within the threshold distance sum to 1 (Haining 2003). We used Moran's *I* tests to evaluate the spatial autocorrelation of the model residuals, with larger absolute values indicating higher spatial autocorrelation. The three model types account for spatial-autocorrelation in the response variable (*spatial lag*), error term (*error dependence*), and both predictor and response variables (*mixed*) (Anselin 1988). Model fits and coefficients as well as performance in reducing spatial autocorrelation were similar between the three types of models. We report results exclusively for lag models incorporating the 800 km neighbourhood, which yielded the best fit. Approximate global Moran's *I* tests were used to assess the performance of the spatial autoregressions in reducing spatial autocorrelation (Haining 2003). Likelihood ratio tests were applied to test the significance of spatial autocorrelation coefficients.

Phylogenetic relatedness is an additional source of data non-independence. We account for phylogenetic covariation using generalized least squares regressions (GLS), in which expected variances of and correlations between error terms are derived from phylogenetic topology and branch lengths (R packages ape and PHYLOGR, Garland *et al.* 2005). We built a phylogeny based on Pough *et al.* (2001) to the familial level and subsequently incorporated taxonomic classifications as star phylogenies assuming equal branch lengths. The GLS method required restricting the analysis to one randomly selected observation for each of the database's 115 island and 223 mainland species. We tested for phylogenetic correlation using Pagel's (1999) λ, which ranges between 0 (phylogenetic independence) and 1 (species traits covary in direct proportion to their shared evolutionary history).

RESULTS

Density compensation is a general and global phenomenon: on average lizards on islands have population densities (*N*, lizards ha^{-1}) that are over an order of magnitude higher than on the mainlands ($N_{island} \approx 10^{1.31 \pm 0.08} N_{mainland}$; $F_{[1,641]} = 271.5$, $P < 1 \times 10^{-15}$). While on mainlands, lizard species occur on average at a density of 128 (± 56)

individuals ha^{-1}, the average is 1920 (± 574) individuals ha^{-1} on islands. For example, populations of lizards in the genus *Anolis* are nearly an order of magnitude more dense on Caribbean islands than in the adjacent Central American mainland despite reasonably similar environmental conditions ($N_{island} \approx 10^{0.96} N_{mainland}$).

This first analysis ignores the substantial variation in energy needs and availability across lizard populations. In both island and mainland sites, lizard population densities (lizards ha^{-1}) decline as a power law of energy use, *B*, suggesting a strong and general role of energetic constraints (mainland: $N \propto B^{-0.78 \pm 0.05}$; island: $N \propto B^{-0.78 \pm 0.11}$, Fig. 1). The indistinguishable slopes indicate that the distribution of energy use between lizard species of different sizes is similar among mainlands and among islands. However, the slopes are somewhat shallower than the slopes of −1 expected if energy use fully accounts for densities and if the populations use equal amounts of energy, as has been observed for other taxa (Damuth 1987). The different intercepts suggest that island lizard populations receive more energy than mainland
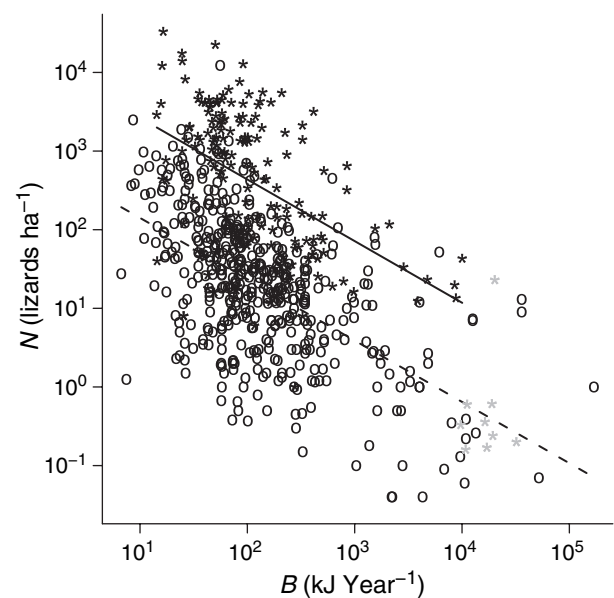

Figure 1 The power-law relationships between log annual energy use, *B* (kJ year^{-1}), and log lizard population density, *N* (lizards ha^{-1}): $N \propto B^{-0.78 \pm 0.05}$ ($F_{[1,468]} = 228.6$, $P < 1 \times 10^{-15}$, $r^2 = 0.33$) for mainland sites (open circles, dashed line) and $N \propto B^{-0.78 \pm 0.11}$ ($F_{[1,171]} = 48.5$, $P < 1 \times 10^{-10}$, $r^2 = 0.22$) for islands (stars, solid line). While the slopes are similar, the island intercept is significantly higher ($10^{3.43 \pm 0.24}$ vs. $10^{2.15 \pm 0.11}$ lizards ha^{-1} for a species with a metabolism of 10 kJ year^{-1}). Energy use, *B*, was calculated by summing over each hour of an average day of each month. The largest island lizards (grey stars, > 1500 g) were omitted from the regression because the majority were identified as low-density outliers.

lizard populations (intercepts: $10^{3.43\pm0.24}$ vs. $10^{2.15\pm0.11}$ lizards ha^{-1} for a species with a metabolism of 10 kJ year^{-1}).

We next control for the amount of available energy (as estimated with net primary productivity, P, t C ha^{-1} year^{-1}, Meehan *et al.* 2004). Energy availability significantly constrains population density ($\log_{10} N \propto -0.68(\pm 0.05) \log_{10} B + 0.71(\pm 0.06) \log_{10} P$; $F_{[2,640]} = 193.1$, $P < 1 \times 10^{-15}$, $r^2 = 0.37$). Environmental constraints apply similarly to island and mainland lizard populations and are unable to explain the vastly higher densities on islands. Even after statistically controlling for energetic constraints (B and P), lizard densities are consistently an order of magnitude greater on islands than on mainlands (Fig. 2, $N_{\mathrm{island}} \approx 10^{1.07\pm0.08} N_{\mathrm{mainland}}$; $F_{[3,639]} = 236.3$, $P < 1 \times 10^{-15}$, $r^2 = 0.53$). This is particularly clear when examining the increase in standardized lizard density from the southern mainland US to the Caribbean Islands, a region of reasonably similar environmental conditions (Fig. 2 inset).

Repeating the analysis to account for spatial autocorrelation using maximum-likelihood spatial autoregressive models confirms the robustness of these findings. Model coefficients are similar, but somewhat lower, when accounting for spatial autocorrelation (Table 1, note that depressed coefficients can result from imperfect determination of the spatial matrix, Haining 2003). Model coefficients and explanatory power are similar when excluding *Anolis* lizards, which have been thought to be exceptionally dense (Wright 1981). When family is considered a random effect in a mixed effect model controlling for energetic constraints (B and P), lizard densities remain an order of magnitude greater on islands than on mainlands ($N_{\mathrm{island}} \approx 10^{1.02\pm0.14} N_{\mathrm{mainland}}$, see Tables S1 and S2 for further evidence that the observed magnitude of density compensation is robust to phylogeny).

We now investigate the hypothesized ecological drivers of higher island densities. On average, island sites have much lower richness of competitor and predator species ($P < 0.001$, *t*-tests, Fig. 3a,d), which is consistent with the occurrence of density compensation. We first evaluate the potential for reduced competition for arthropods to drive density compensation for the majority of lizards, which are
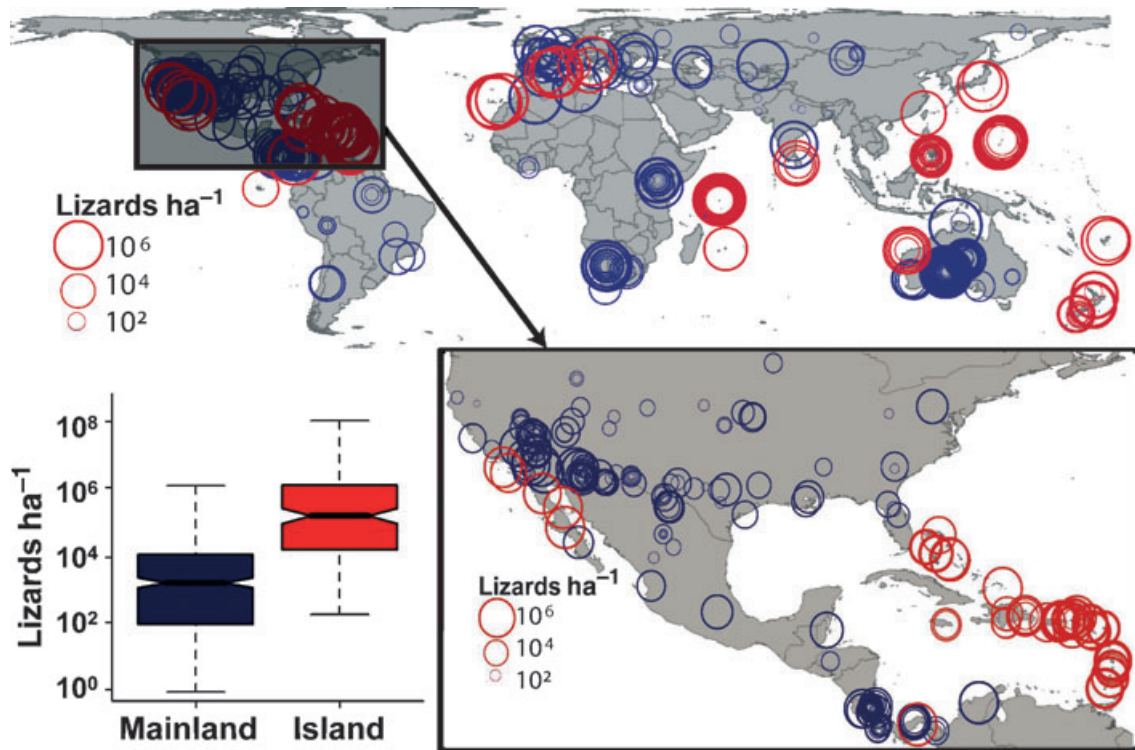

Figure 2 The one order of magnitude difference in standardized lizard density (N_s, lizards ha^{-1}) between mainlands and islands. Numbers are from the model controlling for energy use (B, kJ year^{-1}) and supply (P, minimum net primary productivity) and are standardized for a 10 g lizard at 20 °C and 0.60 t C ha^{-1}year^{-1} minimum productivity (as typical for a location in Central US or Central Europe). Densities are log scaled and binned into 25 equal intervals and larger circles indicate higher standardized densities for islands (red) and mainland (blue). The statistical model developed to standardize lizard densities includes a binomial island factor, I ($N_p = 2.95 - 0.73\ B + 0.29\ P + 1.07\ I$), but standardized densities are plotted as though all sites are mainland [$N_s = N_p(m = 10\ g, t = 20\ °C, P = 0.60\ t\ C\ ha^{-1}\ year^{-1}, I = 0)^* N_e/N_p(m_e, t_E, P_e, I = 0)$, where N_e is empirically observed lizard density]. Note that this standardization will depict large lizards in low productivity regions as having exceptionally high densities. The boxplot (data range, quartiles, 95% confidence intervals for the mean) depicts standardized densities.

Table 1 Ecological models of lizard population density (lizards ha^{-1}) across islands and mainlands and for each group independently

Effect	Non-spatial					Spatial			
	b	t	AIC	r^2	I	b	z	AIC	I
Combined mainland and islands									
COMP (SR$_{comp\ all}$)	−1.05	−11.08***	1498.9	0.48	0.30	−0.41	−4.53***	1320.1	0.02
PRED (SR$_{pred\ all}$)	−0.78	−12.73***	1466.5	0.50	0.28	−0.37	−6.05***	1313.1	0.02
BOTH (SR$_{Comp\ all}$+SR$_{pred\ all}$)	−0.07	−0.38	1468.4	0.50	0.27	0.08	0.49	1314.7	0.02
	−0.74	5.76***				−0.40	−3.34***		
Mainland									
COMP (SR$_{comp\ all}$)	0.28	1.63	1015.7	0.37	0.06	0.01	0.02	967.3	−0.10
PRED (SR$_{pred\ all}$)	−0.01	−0.03	1018.4	0.36	0.08	−0.11	−0.71	966.8	−0.10
BOTH (SR$_{comp\ all}$ +SR$_{pred\ all}$)	0.42	2.08*	1016.0	0.37	0.05	0.11	0.59	968.5	−0.11
	−0.27	−1.30				−0.18	−0.91		
Islands									
Area (10^4 km^2)	−0.21	−5.19***	396.4	0.33	0.24	−0.18	−4.93***	357.8	−0.02
COMP									
SR$_{comp\ birds}$	−0.96	−6.32***	385.2	0.37	0.21	−0.64	−4.01***	364.0	−0.03
SR$_{comp\ mammals}$	−0.54	−2.65**	414.9	0.26	0.24	−0.37	−2.04*	376.4	−0.03
SR$_{comp\ lizards}$	−0.51	−5.16***	396.7	0.33	0.18	−0.28	−2.83**	373.0	−0.03
SR$_{comp\ all}$	−1.19	−7.17***	376.0	0.41	0.12	−0.78	−4.24***	363.5	−0.04
PRED									
SR$_{pred\ birds}$	−0.68	−4.10***	405.5	0.30	0.24	−0.22	−1.38	378.7	−0.01
SR$_{pred\ mammals}$	−0.50	−2.78**	414.2	0.26	0.23	−0.24	−1.51	378.3	−0.03
SR$_{pred\ snakes}$	−0.52	−5.92***	389.3	0.36	0.21	−0.29	−3.09**	371.1	0.00
SR$_{pred\ all}$	−0.55	−5.46***	393.9	0.34	0.23	−0.28	−2.64**	373.6	0.01
BOTH (SR$_{comp\ all}$ + SR$_{pred\ all}$)	−2.05	−4.88***	373.0	0.42	0.05	−1.50	−3.86***	351.4	−0.11
	0.54	2.22*				0.49	2.18*		

Models include energy use (B, kJ year^{-1}) and supply (P, annual minimum net primary productivity) and competitor (COMP), predator (PRED), or combined (BOTH) SR (Table S5). Smaller AIC values indicate better models. The AIC values can be compared to those of the null model ($N \propto B + P$) for each group (combined: 1609.9, 1527.3; mainlands: 1016.0, 965.3; islands: 420.0, 376.9 for the non-spatial and spatial models, respectively). Spatial autocorrelation is accounted for using lag models with an 800 km neighbourhood. Higher absolute values of Moran's I indicate stronger spatial autocorrelation. Statistically significant at *$P < 0.05$; **$P < 0.01$; ***$P < 0.001$.

insectivorous (Vitt & Pianka 2005). As predicted, the combined richness (SR) of insectivorous birds, mammals and lizards significantly accounts for density compensation when incorporated in energetic models (Table 1). The magnitude of the island factor decreases ($N_{island} \approx 10^{0.38 \pm 0.07} N_{mainland}$; $F_{[1,641]} = 32.7$, $P < 1 \times 10^{-7}$) when competitor SR is included in the energetic model. Insectivorous birds are the dominant taxa driving competitive release, whereas lizard richness has relatively little influence on lizard population density (Table S3).

A second mechanism leading to density compensation may be release from predation by carnivorous birds, mammals and snakes. The combined predator richness significantly accounts for density compensation when incorporated in energetic models (Table 1). The predator release effect is similar to that of competitor release and also accounts for much of the variation explained by island ($N_{island} \approx 10^{0.29 \pm 0.07} N_{mainland}$; $F_{[1,641]} = 19.2$, $P < 1 \times 10^{-4}$). Predatory birds are the dominant driver of predatory release (Table S3). We note that accounting for competitor and predator richness does not affect the scaling of population density with environmental constraints (Table S4).

Distinguishing the importance of competitive and predatory release among mainland and island sites is hampered by the strong collinearity of these predictors (SR$_{predatory\ birds} \propto$ SR$_{competitive\ birds}^{0.80 \pm 0.02}$; $F_{[1,641]} = 2011.0$, $P < 1 \times 10^{-15}$, $r^2 = 0.76$). Considering both competitor and predator richness together does not significantly improve the energetic model fit over their individual effects (Table 1). We conclude that either predatory or competitive release is dominant, but relative strength cannot be distinguished when the data for islands and the mainland are considered together. We next examine mainland and island populations separately to assess the relative strengths of predator and competitive release. Mainland lizard population densities are at most weakly correlated with predator and competitor richness (Table 1, Fig. 3b,e). This is despite the substantial observed variation of 19–457 and 17–185 competitor and predator species, respectively.
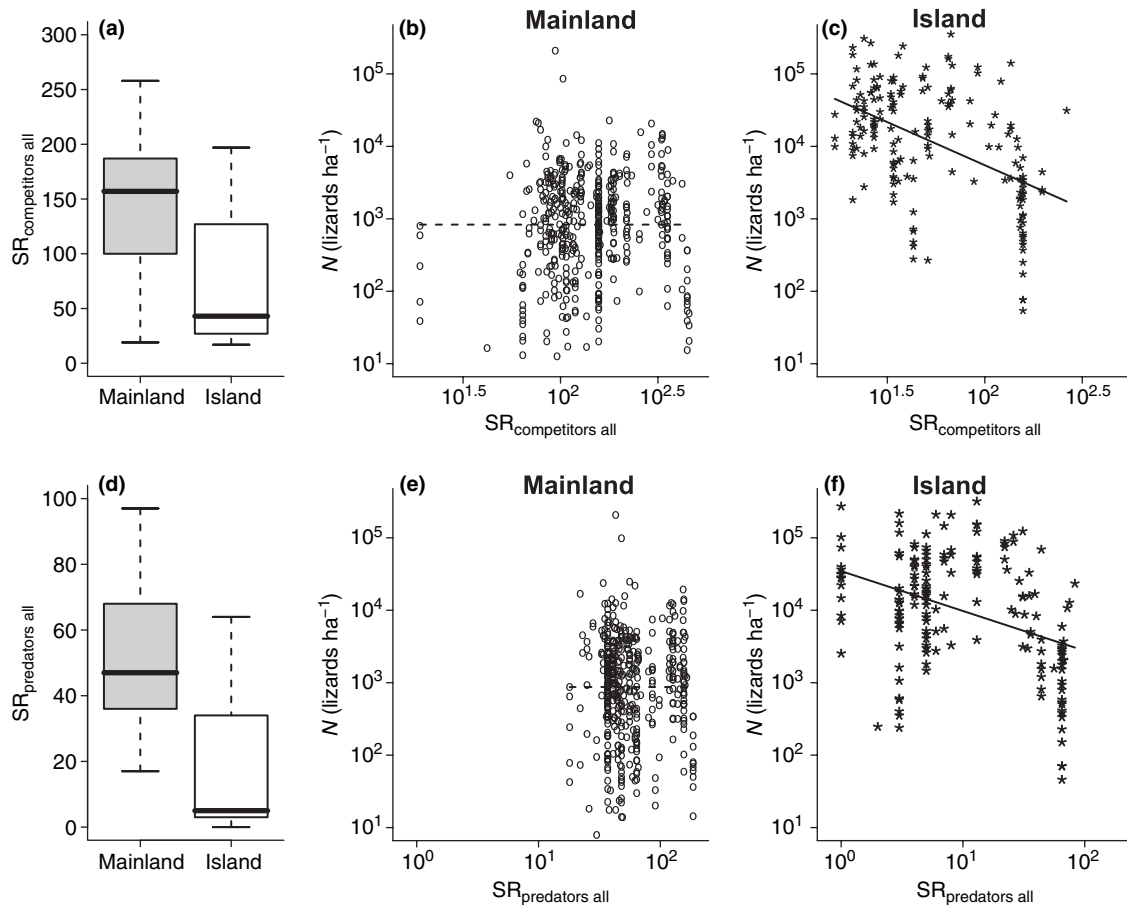
Figure 3 A comparison of the species richness of (a) competitors and (d) predators across mainland and island populations (5, 25, 50, 75 and 95% quantiles depicted). The influences of competitor and predator richness on standardized lizard densities (lizards ha^{-1}), i.e. controlled for energy use and supply ($B + P$), are shown for the mainland (b, e, open circles, dashed lines) and islands (c, f, stars, solid line). Competitor richness (SR$_{competitors\ all}$) is the summed richness of potentially competing insectivorous bird, mammal and lizard species. Predator richness (SR$_{predators\ all}$) is the summed richness of potentially competing predatory bird, mammal and snake species.

Among islands, we first investigate whether island area, a core determinant of island SR (MacArthur & Wilson 1967), correlates with the degree of density compensation. Greater density compensation is observed on smaller islands, but island size *per se* is a weaker predictor than competition and predation proxies in the non-spatial models (Table 1). Both competitor and predator richness can independently account for density compensation on islands (Table 1, Fig. 3c,f). However, when the richness of both guilds are included in the energetic model, competitive release is a stronger determinant of density compensation. In the combined model, island lizard density decreases with increased competitor richness but increases (in a less significant and weaker manner) with predator richness (Table 1). In the combined model or with only competition included in the model, island size (A, 10^4 km^2) is no longer a significant predictor of lizard density ($N_{island} \propto A^{-0.04\pm0.04}$; $F_{[1,171]} = 1.2$, $P = 0.3$; $N_{island} \propto A^{-0.05\pm0.04}$; $F_{[1,171]} = 1.6$,

$P = 0.2$, respectively), but it retains significance when predation alone is fitted ($N_{island} \propto A^{-0.10\pm0.04}$; $F_{[1,171]} = 6.3$, $P < 0.01$).

We confirm that our findings at the global scale also apply to a particular region, North America and the Caribbean. While the best available data for lizard and snake richness is at the ecoregion scale for some regions, richness in North America and the Caribbean is based exclusively on range maps and island-specific species lists. Findings for North America and the Caribbean may differ from those at the global scale because Caribbean lizard populations are thought to be exceptionally dense and the Caribbean islands have broadly similar predator and competitor communities. We find that the island factor is indeed substantially larger when only considering North America and the Caribbean and controlling for energy use and availability ($N_{island} \approx 10^{1.42\pm0.19} N_{mainland}$; $F_{[3,233]} = 182.1$, $P < 1 \times 10^{-15}$). Competitor richness is a highly significant predictor of density

when included in a model with energy use and availability ($t = -7.3$; $P < 1 \times 10^{-11}$) as is predator richness ($t = -10.5$; $P < 1 \times 10^{-15}$). The magnitude of the island factor decreases but does significantly account for the residuals of the energetic model with competition ($N_{island} \approx 10^{0.62 \pm 0.19} N_{mainland}$; $F_{[1,235]} = 41.5$, $P < 1 \times 10^{-9}$). A significant but lesser island factor is likewise observed for residuals of the model with predation ($N_{island} \approx 10^{0.35 \pm 0.18} N_{mainland}$; $F_{[1,235]} = 3.7$, $P < 1 \times 10^{-3}$). We also confirm that competition and predation with birds has a stronger effect on lizard densities than either lizards or snakes for North American and the Caribbean. When accounting for energy use and availability, bird competition (effect = -2.16 ± 0.55; $F_{[3,233]} = 95.2$, $P < 1 \times 10^{-15}$; $r^2 = 0.55$) and predation (effect = -1.68 ± 0.35; $F_{[3,233]} = 111.2$, $P < 1 \times 10^{-15}$; $r^2 = 0.58$) better account for higher island lizard densities than do lizards (effect = -0.36 ± 0.25; $F_{[3,233]} = 64.5$, $P < 1 \times 10^{-15}$; $r^2 = 0.45$) or snakes (effect = -0.93 ± 0.24; $F_{[3,233]} = 95.6$, $P < 1 \times 10^{-15}$; $r^2 = 0.55$).

DISCUSSION

This combined mainland–island analysis helps resolve the long-standing question of whether ecological or environmental constraints predominantly determine animal population densities. While mainland sites show substantial variation in the number of predators and competitors, this variation has little effect on species' abundances. This suggests that ecological pressures (at least as reflected in competitor and predator richness) do not strongly influence mainland densities. External drivers (such as energy/prey availability) may determine the richness of both lizards and the species they interact with and maintain a constant role of ecological constraints across mainland sites. Emigration and immigration can dampen ecological perturbations in accessible, open systems more readily than those in more isolated systems such as islands (MacArthur & Wilson 1967).

In contrast, while following similar environmental constraints as their mainland counterparts, island populations are strongly driven by release from ecological constraints. Ecological release explains both an order of magnitude higher densities on islands and substantial between-island variation. While the partitioning of energy between lizard species of different sizes is constant between islands and mainlands, island lizard populations use more energy than mainland lizard populations. Ecological differences between islands and mainlands may contribute to the higher energy use by island populations. For example, Olesen & Valido (2003) suggest that islands have fewer arthropods available to lizards and hence a high frequency of herbivorous lizards. Lizards eating at a lower trophic rank have potential to reach higher population densities (Pough 1973).

Notably, we find that birds more strongly influence lizard densities than do other lizard species. The importance of birds in ecological release can be broadly explained by greater insular extinction rates for birds than lizards (Case 1975; Wright 1981). Differential extinction rates between taxa can result in lizard communities, and not just populations, receiving more energy on islands than on mainlands. Additionally, the influence of other lizard species on lizard density may have been reduced by past competition causing lizard species to evolve to minimize resource competition (i.e. the ghost of competition past, Connell 1980). Field studies have confirmed our finding that avian competition can be a stronger determinant of lizard density than avian predation (Wright 1979, 1981), but avian predation has been shown to regulate lizard density on some small islands (Schoener & Schoener 1978). The predictive power of predator richness may be reduced by predators that exert stronger predation pressure on species that eat lizards than lizards themselves, indirectly benefiting lizards (Case 1994).

While reduced competitor and predator richness does account for higher densities on islands, substantial density variation remains (Fig. 3). The significant phylogenetic autocorrelation observed for some particular predator and competitor taxa leads to the ecologically interesting conclusion that these taxa differentially prey upon or compete with different lizard groups, which could be a source of density variation. Temporal variability is unlikely to contribute substantially to the scatter in the relationship because lizard populations are markedly constant through time (Schoener 1994). Clearly, the different broad-scale effects included in the model are strong, but not perfect correlates of the conditions individuals encounter at the local scale. As in all analyses at this scale, methodological differences across studies likely contribute additional noise. Importantly, this residual variation is independent from the focal effect of insularity, and the strong trends above and beyond highlight its prominence.

We demonstrate that at least for lizards density compensation is a ubiquitous and global phenomenon. Similar findings across global and regional scales support the ubiquity of density compensation. Local evidence for other groups suggests the potential to generalize our results across taxa (MacArthur et al. 1972; Tonn 1985; Sara & Morand 2002). However, meta-analysis indicates that density compensation may be uncommon and its occurrence may vary by taxa (Connor et al. 2000). While densities of birds and insects generally increase with area, mammals showed little relationship (Connor et al. 2000). Lizards may have an exceptional potential to reach high densities following predator and competitor release due to their relative low energetic costs, which can be up to 10 times lower than those of endotherms (Pough 1980). Lizards may also

increase their densities by diversifying their diets (Olesen & Valido 2003). While the ubiquity of density compensation across taxa is uncertain, our finding that the degree of resource partitioning strongly influences island densities is likely to be general.

Insularity dramatically alters the balance of environmental and ecological constraints on population density. This confirms the gravity of the threat that species introductions and climate-induced range shifts pose to island endemics, which have limited evolutionary experience with predation and competition. Many case studies have illustrated the dramatic impact certain introduced species can have on island biota, e.g. mongooses on island lizards (Case & Bolger 1991) or snakes on breeding birds (Rodda *et al.* 1997). Our results confirm that island invasions or losses of even single species may dramatically alter abundances of interacting species. More generally our findings demonstrate and put into a broader framework the elevated sensitivity of island biota to even small ecological perturbations. The distinct vulnerability of islands will likely be of considerable importance in our future world of rapid environmental change.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available online for this article:

Appendix S1 Database literature sources.
Appendix S2 Analyses of potential data biases.
Table S1 Ecological models of lizard population density (lizards ha^{-1}) across islands and mainlands and for each group independently accounting for phylogenetic autocorrelation.
Table S2 Coefficients for predator and competitive release models accounting for phylogenetic autocorrelation.
Table S3 Models examining the influence of the richness of different taxa on combined mainland and island lizard densities.
Table S4 Coefficients for models examining the influence of taxa richness on combined mainland and island lizard densities.
Table S5 Coefficients for predator and competitive release models explaining lizard densities.

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