RESEARCH PAPER

Power in numbers. Drivers of high population density in insular lizards

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ABSTRACT

Aim Islands organisms usually have fewer predator and competitor species than mainland ones. This is thought to result in high population densities on islands. We hypothesize that insular lizards have denser populations than mainland species and that density, in general, is negatively correlated with competitor and predator richness.

Location Global.

Methods We compared densities of 346 lizard species on islands and the mainland while examining the relationship between density and, predator and competitor richness, primary productivity, seasonality and island area. We controlled for phylogenetic non-independence, body mass and study area, which are known to strongly affect population density.

Results Insular populations (especially on snake-free islands) are denser than mainland ones. Mainland populations of lizard species that also inhabit islands were denser than those of species that do not inhabit islands. Population density was the highest on islands with low net primary productivity and was not significantly affected by competitor or predator richness. Moreover, insular populations show high density regardless of island area.

Main conclusions We conclude that the ability of mainland species to reach high population densities may increase their chances in reaching and successfully colonizing islands. We postulate that population density may be affected by predator and competitor density rather than by their richness. Density increase on islands may result not from the environmental simplicity of island faunas but through propagule sorting or pressure.

Keywords

Density compensation, dispersal, ecological sorting, insularity, lizards, population density, snakes.

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INTRODUCTION

Species on islands tend to have population densities that are higher by about an order of magnitude than those of closely allied mainland species (MacArthur *et al.*, 1972; Blondel, 2000; Rodda & Dean-Bradley, 2002; Buckley & Jetz, 2007) or even of the same species (e.g. *Anolis limifrons*, Andrews, 1979; *Antechinus minimus*, Sale & Arnould, 2012). MacArthur *et al.* (1972) showed that there are fewer species of birds on islands, but these species have high population densities. This results in a nearly equal density to that in a similar mainland patch. They called this phenomenon 'density compensation'. Much research has been carried out on the population density of various taxa in both interspecific and intraspecific frameworks (e.g. MacArthur *et al.*, 1972; Andrews, 1979; Blondel, 2000). The results of several large-scale studies have supported the generality of high population densities in insular species and of density compensation (Buckley & Jetz, 2007; Novosolov *et al.*, 2013). Though most insular species show a high population density, actual density can vary among species depending on, for example, body size and environmental factors (MacArthur *et al.*, 1972; Blondel, 2000; Novosolov *et al.*, 2013).

Low interspecific competition and low predation risk have been posited as possible factors increasing population density in insular species (MacArthur *et al.*, 1972; Adler & Levins, 1994). On an island, the available resources are divided between fewer species, therefore increasing the average share of energy consumed by members of each species (Adler & Levins, 1994; Pafilis *et al.*, 2009a). This, together with low interspecific predation pressures, means that carrying capacity is increased for a given species. Low interspecific competition and predation may also lead to character release in insular species by allowing them to expand their niche, either by increasing the resource exploitation of each individual or through niche shift in which different individuals from the same species specialize on different resources (MacArthur *et al.*, 1972; Case, 1975; Bolnick *et al.*, 2007, 2010). By expanding their niche, populations of insular species can further increase their densities (Bolnick *et al.*, 2010).

Population density can be affected by the amount of resources available (White *et al.*, 2007). Islands tends to have stable climates (Whittaker & Fernandez-Palacios, 2007), which may also facilitate high population densities (Adler & Levins, 1994; Whittaker & Fernandez-Palacios, 2007). Individual mortality decreases in more stable environments, and this is one contributor to population density (Adler & Levins, 1994). Net primary productivity (NPP) is considered to be a good proxy of the amount of available resources (Evans *et al.*, 2005). Islands are often portrayed as having low productivity (MacArthur & Wilson, 1967, Palkovacs, 2003, cf. Meiri & Raia, 2010), and thus NPP may have a strong statistical association with population density.

We study factors that may affect population density on islands. We focus on lizards, an extremely diverse and widely distributed group (Pianka, 1995; Blackburn, 2006; Losos, 2009). Lizards are ubiquitous on many islands as well as on all but the coldest mainland regions, occupying a variety of habitats (Pianka, 1995). We compared population densities of insular species, species found exclusively on the mainland, and mainland populations of species distributed on both islands and the mainland (mainland 'non-endemic') to better understand the evolution of high population density on islands. In addition, we examined the effects of predation and interspecific competition, primary productivity, island area and climate stability on population density.

We hypothesized that population density would be highest in insular species on small islands and lowest in mainland species regardless of whether they also have an insular population (Buckley & Jetz, 2007; Novosolov *et al.*, 2013) because the number of predators and competitors is lowest on small islands. We hypothesized that population densities would be negatively correlated with predator and competitor richness because low competition and predation allows species to better use the available resources while having decreased mortality rates (MacArthur *et al.*, 1972; Adler & Levins, 1994). These advantages are associated with islands, but should be weaker on large islands which have an environment more similar to that of mainland habitats (Whittaker & Fernandez-Palacios, 2007). Thus, we hypothesized that the density of insular populations would decrease with increase in island area. Moreover, we hypothesized that population density would show a positive relationship with NPP and climate stability, because stable climate and abundant resources allow populations to thrive by increasing their reproductive success and lowering mortality (Adler & Levins, 1994; White *et al.*, 2007).

MATERIALS AND METHODS

We collected data on the population density of 346 lizard species from the primary literature (Appendix S1). We divided these species into four groups based on the distribution of the species and where the species population density data were collected from (hereafter 'distribution groups'): (1) species found only on the mainland (hereafter mainland 'endemics'; $n = 171$); (2) insular endemic species ($n = 117$). We classified species found on both continents and islands as either (3) 'insular non-endemics' ($n = 31$) if our density data for them were estimated on an island, or (4) 'mainland non-endemics' ($n = 27$) if our density data for them were estimated on the mainland (Fig. 1).

The size of the area in which density is estimated strongly and negatively affects estimates of population density (Blackburn &
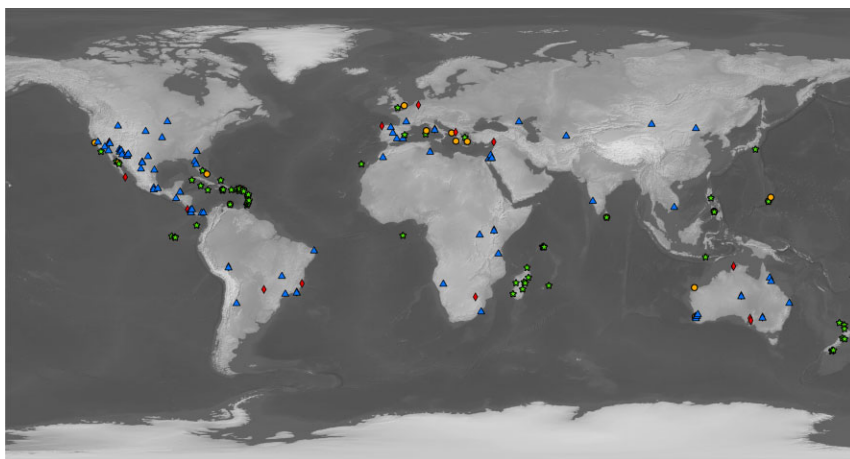

Figure 1 Distribution of insular endemics (stars), insular non-endemic (circles), mainland 'endemics' (triangles) and mainland 'non-endemic' (diamonds) lizard populations in our dataset.

Gaston, 1996). Thus, for each species we recorded the area (in hectares) of the study plot over which population density was calculated (hereafter 'study area'). Populations for which the study area was not reported were excluded. For all insular populations we further collected data on the area (km²) of the island that density was recorded on. To account for the possible effect of body size on population density we collected the mean snout–vent length (SVL) of females for each species, using the primary literature and field guides. When data for females were not available we used male mean SVL. We then transformed SVL to body mass using family-specific equations. For *Liolaemus* and *Phymaturus* we used equations from Pincheira-Donoso *et al.* (2011). For gecko families and for *Anolis* we used the equations in Novosolov *et al.* (2013). For legged anguids we used equations from Meiri *et al.* (2013). For all other species we used family-specific equations from Meiri (2010), differentiating between legless, leg-reduced and legged species (Appendix S2).

We obtained the coordinates of where each population was observed based on the researchers' description of the study area. For species for which we had population density data from more than one locality, we chose the one with the largest study area, because this provides a better density estimation (Blackburn & Gaston, 1996).

We used lizard distribution maps generated by the GARD project (http://www.gardinitiative.org/) to determine lizard species richness for continents and large islands (> 50,000 km²). This was done by first determining the identity of an equal-area Behrmann projection 1° × 1° grid cells that represent the localities of each population density datum (using ArcGIS 10.0, distributed by ESRI). We then spatially joined the layer of lizard species distribution maps to the Behrmann grid to assess species richness in each cell. We used the distribution shapefiles for birds (BirdLife International & NatureServe, 2013), mammals (IUCN Red List 2014; http://www.iucnredlist.org/technical-documents/spatial-data) and snakes (Feldman, 2014) to determine the number of potential predators for each mainland and large island population in our study. To achieve this, we first pruned the data to include only potential lizard predators by excluding all herbivorous and insectivorous birds and mammals and 'blind snakes' (Scolecophidia; Appendix S3). Because distribution maps are often not detailed enough to determine whether a species inhabits a particular small island, we used the primary literature to determine the species richness of native lizards, snakes, carnivorous mammals and invasive species of these groups on all islands < 50,000 km² (Appendix S1). When we found no records on the presence of snakes or mammals on these islands we assumed they were absent from them. Birds are not as limited by island boundaries as are flightless animals, which increases their inter-island distribution potential. We therefore did not collect additional data on bird richness for small (< 50,000 km²) islands, but rather used the known data from species distribution maps created by BirdLife (BirdLife International & NatureServe, 2013).

Using these lists we calculated a 'predation index' by summing the richness, per grid cell, of all three groups. We used this index to examine the impact of predator richness on the insular and mainland population densities. Using these distribution data we determined which islands were free of snakes or mammals. This allowed us to create a presence/absence index for each. Birds were found on all the study islands regardless of island area. Thus we did not create a dichotomy for avian predators.

To determine the NPP value in the areas where population densities were measured, we used log-transformed NPP data from Imhoff *et al.* (2004). We used temperature seasonality (measured as the coefficient of variation of temperature in the different months of the year) as a proxy for climate stability and calculated it for each population using raster data from WorldClim (http://www.worldclim.org/; Hijmans *et al.*, 2005).

Statistical analyses

All variables were $\log_{10}$-transformed to normalize the model's residual distribution and reduce heteroscedasticity. We examined the relationship between population density and competitor richness, predator richness (or presence), NPP and climatic stability. We first determined whether the islands in our dataset indeed contained a unique environment by comparing lizard species richness, predator richness, NPP and temperature seasonality on the islands from which our density data originated with those of the mainland regions for which we had lizard density data using ANOVA tests. We then used ANCOVA analyses to determine how population density varied among the four distribution types while accounting for body mass (g) and study area (ha). Following this, we incorporated into the ANCOVA model the relevant environmental characteristics. We left the 'distribution type' groups in the model even when this was not significant, as it was our primary predictor. Preliminary results (not shown) showed no significant difference between population densities of insular endemic species and those of insular non-endemics (distribution groups types 2 and 3 above). We therefore merged these groups for the rest of the analyses. Addition of invasive species to the sum of potential predators did not change the results qualitatively (not shown). Thus we report results obtained for native species only throughout the rest of the text.

We repeated the ANCOVA analyses for insular populations and mainland populations separately, while still accounting for differences between mainland 'endemics' and mainland 'non-endemics'. When examining only the insular populations we incorporated island area and the presence (or absence) of snakes and mammals as additional predictors. We chose the best model based on *P*-values (at $\alpha = 0.05$).

Species traits are known to be phylogenetically conserved (Felsenstein, 1985). To account for phylogenetic non-independence we used the phylogeny for squamates published by Pyron & Burbrink (2014), pruned for the species in our study. We repeated all analyses using phylogenetic generalized least square (PGLS) regression and ANCOVA (Freckleton *et al.*, 2002). PGLS models provide 'pseudo-R^2' values that are usually obtained from different models (Symonds & Blomberg, 2014). Thus, they may not be strictly comparable to R^2 values obtained using non-phylogenetic methods. We corrected the branch

lengths of the phylogenetic tree using the maximum likelihood value of the scaling parameter λ (Pagel, 1997) implemented in the R package 'Caper' (Orme, 2014). All statistical analyses were done in R (R Core Team, 2014).

RESULTS

As expected, islands in our sample had fewer lizard species, fewer predator species (together and separately for snakes, mammals and birds), less variation in seasonal temperatures and lower NPP than the mainland areas (Table 1).

Lizard population density decreased with increasing body mass and study area. (Phylogenetic model: intercept, 1.85 ± 0.4; mass–slope, -0.32 ± 0.09; $t = -3.43$, $P < 0.002$; study area–slope, -0.44 ± 0.05, $t = -8.16$, $P < 0.002$; $R^2 = 0.22$. Non-phylogenetic model: intercept, 1.52 ± 0.1; mass–slope, -0.23 ± 0.07; $t = -3.21$; $P = 0.001$; study area–slope, -0.53 ± 0.05; $t = -9.29$; $P < 0.002$; $R^2 = 0.29$.) Study area alone, the strongest predictor, explained 19% of the variation in density (27% in the non-phylogenetic model).

Population density is phylogenetically conserved (maximum likelihood $\lambda = 0.7$). Species on islands had the highest population density (mean = 158 individuals ha^{-1}; Table 2a, Fig. 2), mainland 'endemic' species had the lowest densities (mean = 18.2 individuals ha^{-1}; Table 2a, Fig. 2) and mainland 'non-endemics' showed intermediate population densities (mean = 50.1 individuals ha^{-1}; Table 2a, Fig. 2), corrected for mass (phylogenetic model slope -0.41 ± 0.08, $t = -4.87$, $P < 0.002$; non-phylogenetic model slope -0.34 ± 0.07, $t = -5.03$, $P < 0.002$) and study area (phylogenetic model slope -0.36 ± 0.05, $t = -7.04$, $P < 0.002$; non-phylogenetic model slope -0.38 ± 0.06, $t = -6.7$, $P < 0.002$; Fig. 2). These results were consistent in both the phylogenetic and the non-phylogenetic models.

When incorporating environmental factors into the model we found that population densities of insular species and mainland 'non-endemics' were similarly higher than that of mainland 'endemics' (Table 2b), corrected for mass (phylogenetic model slope -0.42 ± 0.08, $t = -5.21$, $P < 0.002$; non-phylogenetic model slope -0.33 ± 0.06, $t = -5.42$, $P < 0.002$) and study area (phylogenetic model slope -0.34 ± 0.05, $t = -6.88$, $P < 0.002$; non-phylogenetic model slope -0.39 ± 0.05, $t = -7.5$, $P < 0.002$). In addition, population density was negatively correlated with the richness of potential predators and showed marginally non-significant negative correlation with lizard richness (Table 3a). In the non-phylogenetic model population density was negatively correlated with lizard richness and NPP but not with richness of potential predators (Table 3a). Temperature seasonality had no significant effect on population density in either the phylogenetic or the non-phylogenetic model (Table 3a). In the phylogenetic and non-phylogenetic models with environmental factors, insular species and mainland non-endemics had similarly high population density compared with mainland 'endemic' species (Table 3a). These models explained 41% and 51% of the variation in density in the phylogenetic and non-phylogenetic analyses, respectively.

We tested the effect of ecological and environmental attributes on insular and mainland populations separately. Population density was higher on snake-free islands than on those with snakes (snake-free, intercept $- 13.16 \pm 2.05$, $t = 6.42$, $P < 0.002$; snakes present, intercept $- 12.6 \pm 2.2$, $t = 2.8$, $P < 0.002$). Population density on islands marginally decreased with increasing NPP (significantly so in the non-phylogenetic model; Table 3b) and with increasing temperature seasonality (only in the non-phylogenetic model). Corrected for body mass and study area, we found that lizard richness, predator richness and island area had no significant effect on the population density of insular species (Table 3b). The full phylogenetic model explained 39%

		Estimate ± SE	t	P
(a)				
Lizard richness	Mainland	1.53 ± 0.05	37.21	< 0.002
$r^2 = 0.18$	Islands	1.10 ± 0.04		
Predation index	Mainland	2.14 ± 0.03	84.90	< 0.002
$r^2 = 0.49$	Islands	1.75 ± 0.03		
Log NPP	Mainland	11.32 ± 0.04	327.82	< 0.002
$r^2 = 0.04$	Islands	11.14 ± 0.03		
Temperature seasonality	Mainland	3.47 ± 0.02	110.34	< 0.002
$r^2 = 0.13$	Islands	3.18 ± 0.03		
(b)				
Snakes	Mainland	39.9 ± 2.66	16.20	< 0.002
$r^2 = 0.27$	Islands	9.77 ± 2.01		
Birds	Mainland	153.08 ± 7.80	21.92	< 0.002
$r^2 = 0.31$	Islands	55.48 ± 5.90		
Mammals	Mainland	97.01 ± 5.02	20.27	< 0.002
$r^2 = 0.43$	Small Islands	15.24 ± 3.80		

Table 1 Summary of the comparison between mainland and islands, using simple correlation models of: (a) Log10 transformed lizard richness, log 10 transformed predation index (i.e. predator richness), net primary productivity (NPP) and temperature seasonality, and (b) snake richness, bird richness and mammal richness. Mean values of each the above mentioned parameters are reported with standard error, t-values and P-values and r^2 for model fit.

Table 2 Population density of mainland 'endemic', mainland 'non-endemic' and island lizards as a function of study area and mass (a) without any environmental variables and (b) lizard richness and net primary productivity (NPP) in the non-phylogenetic model, and potential predator richness in the phylogenetic model. The intercepts represent the $\log_{10}$ mean population density (individuals ha^{-1}) when the value of all the predictors are zero (on the diagonal). Off-diagonal represents the relationship between different distribution groups (e.g. the population density of mainland 'endemics' is significantly lower than the population density of mainland 'non-endemics' with $t = -2.32$ and $P = 0.02$). Above the diagonal: phylogenetic model, $\lambda = 0.57$, $R^2 = 0.35$. Below the diagonal: non-phylogenetic model, $R^2 = 0.40$.

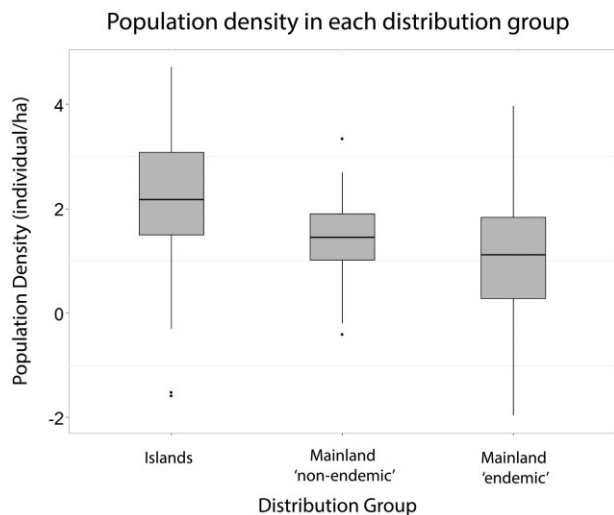|	Mainland 'endemic' ($n = 171$)	Mainland 'non-endemics' ($n = 27$)	Islands ($n = 148$)
(a)			
Mainland 'endemic'	Phylogenetic intercept 1.48 ± 0.34	$t = -2.32$	$t = -8.20$
	Non-phylogenetic intercept 1.25 ± 0.1	$P = 0.02^*$	$P < 0.002^*$
Mainland 'non-endemics'	$t = 2.19$	Phylogenetic intercept 1.91 ± 0.38	$t = -2.84$
	$P = 0.03^*$	Non-phylogenetic intercept 1.7 ± 0.2	$P = 0.004^*$
Islands	$t = 8.14$	$t = 2.44$	Phylogenetic intercept 2.45 ± 0.35
	$P < 0.002^*$	$P = 0.01^*$	Non-phylogenetic intercept 2.19 ± 0.12
(b)			
Mainland 'endemic'	Phylogenetic intercept 3.59 ± 0.53	$t = -2.35$	$t = 3.28$
	Non-phylogenetic intercept 7.21 ± 1.36	$P = 0.019^*$	$P < 0.002^*$
Mainland 'non-endemics'	$t = 2.01$	Phylogenetic intercept 4.01 ± 0.55	$t = -0.34$
	$P = 0.045^*$	Non-phylogenetic intercept 7.59 ± 1.39	$P = 0.733$
Islands	$t = 5.06$	$t = 1.14$	Phylogenetic intercept 4.08 ± 0.46
	$P < 0.002^*$	$P = 0.257$	Non-phylogenetic intercept 7.82 ± 1.36

Figure 2 Median, upper, and lower quantiles of $\log_{10}$ population density (individuals ha^{-1}) for species on islands, mainland 'non-endemic' and mainland 'endemic'.

of the variation in the density of insular species while body mass and study area alone explained 32% (53 and 36%, respectively, in the non-phylogenetic model). On the mainland, population density decreased with increasing lizard and predator richness, corrected for body mass and study area (Table 3c). Mainland 'non-endemic' species have significantly higher population densities than mainland 'endemics' (in the phylogenetic model only: mainland 'non-endemic' intercept 4.55 ± 0.75, mainland 'endemic' intercept 4.15 ± 0.74, $t = 2.04$, $P = 0.04$; non-phylogenetic model, mainland 'non-endemic' intercept 4.18 ± 0.66, mainland 'endemic' intercept 3.88 ± 0.8, $t = 1.56$, $P = 0.12$). Temperature seasonality and NPP had no significant effect on mainland population density in either the phylogenetic or the non-phylogenetic model (Table 3c).

DISCUSSION

In line with our hypothesis and with previous results (Buckley & Jetz, 2007; Novosolov *et al.*, 2013) insular species have higher population densities than mainland species. Surprisingly, mainland populations of species that also inhabit islands have higher population densities than mainland 'endemic' species. Mainland population densities are relatively low where lizard and predator richness are high. Population density was unrelated to any of the environmental characteristics examined on islands, although it was higher on islands without snakes. Overall, we found that population densities on all islands are high, regardless of island area or lizard endemicity.

Population density estimates are lower when estimated over a large area (Blackburn & Gaston, 1996; our results). We found that study area explained more of the variation in population density than body size and any other predictor, indicating that population density estimates are not meaningful when reported without reference to the size of the area over which they were assessed. This trend may be specifically notable in inflating apparent densities of populations surveyed on small islands where the island itself is not much larger than 1 ha.

Table 3 The slopes, *t*-values and *P*-values of the log$_{10}$-transformed environmental predictor variables of population density for (a) all species, (b) only insular species, and (c) only mainland species. The adjusted R^2 values are reported for the best non-phylogenetic ANCOVA and phylogenetic generalized least squares (GLS) models. The maximum likelihood λ is reported for the best phylogenetic GLS model. The significance of the predictor is indicated with and asterisk.

(a)

		Non-phylogenetic($R^2 = 0.48$)			Phylogenetic($R^2 = 0.41$; λ = 0.5)		
Data type	Environmental variable	Parameter estimate	*t*	*P*	Slope	*t*	*P*
All data (*n* = 346)	Lizard richness	−0.56 ± 0.12	−4.72	< 0.002*	−0.22 ± 0.13	−1.71	0.088
	Potential predator richness	−0.33 ±0.21	−1.52	0.128	−0.77 ± 0.20	−3.76	< 0.002*
	NPP	−0.45 ± 0.13	−3.53	< 0.002*	−0.18 ± 0.15	−1.14	0.253
	Temperature seasonality	−0.25 ± 0.15	−1.70	0.089	−0.19 ± 0.17	−1.07	0.287
	Body mass (g)	−0.34 ± 0.06	−5.49	< 0.002*	−0.41 ± 0.08	−5.13	< 0.002*
	Sampling area (ha)	−0.40 ± 0.05	−7.63	< 0.002*	−0.34 ± 0.05	−6.86	< 0.002*

(b)

		Non-phylogenetic($R^2 = 0.53$)			Phylogenetic($R^2 = 0.39$; λ = 0.66)		
Data type	Environmental variable	Slope	*t*	*P*	Slope	*t*	*P*
Only islands (*n* = 148)	Lizard richness	−0.02 ± 0.19	−0.13	0.900	0.12 ± 0.15	0.78	0.430
	Potential predator richness	−0.09 ± 0.25	−0.40	0.700	−0.08 ± 0.28	−0.30	0.760
	NPP	−0.89 ± 0.18	−4.84	< 0.002*	−0.39 ± 0.23	−1.72	0.080
	Island area (km^2)	−0.02 ± 0.06	−0.40	0.700	−0.01 ± 0.06	−0.26	0.800
	Temperature seasonality	−0.46 ± 0.20	−2.21	0.030*	−0.33 ± 0.24	−1.38	0.170
	Body mass (g)	−0.40 ± 0.07	−5.04	< 0.002*	−0.43 ± 0.1	−4.36	< 0.002*
	Sampling area (ha)	−0.27 ± 0.08	−4.02	< 0.002*	−0.29 ± 0.06	−4.80	< 0.002*

(c)

		Non-phylogenetic($R^2 = 0.34$)			Phylogenetic($R^2 = 0.31$; λ = 0.36)		
Data type	Environmental variable	Slope	*t*	*P*	Slope	*t*	*P*
Only mainland (*n* = 198)	Lizard richness	−0.68 ± 0.18	−3.84	< 0.002*	−0.49 ± 0.21	−2.35	0.020*
	Potential predator richness	−0.67 ± 0.28	−2.42	0.016*	−0.89 ± 0.32	−2.80	0.006*
	NPP	−0.10 ± 0.21	−0.46	0.642	0.03 ± 0.23	0.15	0.879
	Temperature seasonality	−0.15 ± 0.36	−0.42	0.674	−0.44 ± 0.37	−1.18	0.240
	Body mass (g)	−0.30 ± 0.09	−3.14	0.002*	−0.38 ± 0.11	−3.65	< 0.002*
	Sampling area (ha)	−0.48 ± 0.07	−6.45	< 0.002*	−0.45 ± 0.07	−6.17	< 0.002*

NPP, net primary productivity.

High population density is hypothesized to be a consequence of island life rather than providing an advantage in colonization (Case, 1975; Buckley & Jetz, 2007; but see Sara & Morand, 2002). We found that mainland populations of species that also inhabit islands are denser than mainland 'endemic' populations. Moreover, population density was quite strongly phylogenetically conserved. Species belonging to certain clades exhibit higher population densities than others under the same conditions. This may indicates that insular communities were established through ecological sorting (Webb *et al.*, 2002; Kraft *et al.*, 2007). Population density might be a proxy for traits such as the ability to exploit resources, reproductive success and territoriality. We

hypothesize that having the potential to reach a high population density on the mainland has allowed these species to successfully colonize islands. Species with high population densities on the mainland may have more potential propagules. This will give them an advantage over rare species in colonizing islands. Furthermore, abundant species may be less prone to extinction when trying to establish viable populations on islands. Once a species reaches an island its population density increases regardless of island area. However, such increase is limited by the presence of snakes, probably due to stronger predation pressure than that found on snake-free islands (Hasegawa, 1994; Paflis *et al.*, 2009b; Calsbeek & Cox, 2010; but see Goessling *et al.*,

2015). In contrast, species colonizing snake-free islands undergo stronger predator release, enabling them to manifest higher population densities.

Islands host fewer species than mainland regions of a similar area, allowing each species to exploit a greater fraction of the available resources and thus to increase its population size (assuming the total amount of resources in a given area is similar, or that the total amount of available resources times the fraction that is available to the population is higher; MacArthur *et al.*, 1972; Whittaker & Fernandez-Palacios, 2007). Larger islands harbour more species, with a possible consequent limit on the population density of each species (Whittaker & Fernandez-Palacios, 2007). Thus, we expected that on large species-rich islands population density would be lower than on small islands with few species (MacArthur *et al.*, 1972). This prediction was not supported: We found no relationship between population density and island area, even when including populations from very large islands such as Madagascar. Moreover, lizard richness and predator richness also did not show any effect on insular population densities. It may be that an increase in species richness, whether it be predator or competitor richness, does not directly affect population density. It is possible that insular environments are more similar to each other, regardless of island size, than has been previously considered. Densities of lizard populations on islands of all sizes appear to be equally susceptible to the same limiting factors. It may be that population density is more affected by factors such as predator and competitor density than by their richness (Meiri *et al.*, 2014). This is partially supported by our findings that species on snake-free islands had higher population densities than species on islands where snake are present.

Islands in our sample have relatively fewer resources than mainland regions. Lizard population density is higher in areas with low NPP, but this difference disappears when phylogeny is accounted for. Resource availability, quantified through NPP, probably affects endotherms much more strongly than ectotherms, which have lower energetic demand (Pough, 1980). Environments with low resource availability cannot usually support many endothermic species (Pough, 1980). In such environments lizards may enjoy little competition and predation from endotherms, allowing population density to increase. This pattern was found only in the non-phylogenetic model, but it does not mean that it is not adaptive: rather it implies that islands with small amounts of resources sort for species with the ability to thrive in these environments.

We suggest that the traits responsible for high population density do not arise in response to the insular environment. Instead, our data suggest ecological sorting of species pre-adapted for island life. Traits promoting high population density facilitate the process of colonization and success on the islands. Species colonizing islands go through selection towards high tolerance to low resource availability. Both the endemic and non-endemic lizard populations on islands are subjected to similar pressures regardless of island area. We hypothesize that insular lizard communities are composed of species that have evolved the ability to increase and maintain their population density. These species showed high population densities on all the islands regardless of area. This study presents the first quantitative evidence showing that high population density on islands arises, at least partially, independently of environmental factors.

ACKNOWLEDGEMENTS

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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.

Appendix S1 The dataset and the metadata (literature sources).
Appendix S2 Species lists and literature sources of mammals, birds and snakes used to estimate predator richness

BIOSKETCH

Maria Novosolov is a PhD student in the Department of Zoology at Tel Aviv University, working under the supervision of Shai Meiri. She is a winner of the Clore fellowship for PhD studies. Her research interests lie in island biogeography and evolution, mainly focusing on global patterns and adaptation of species traits to insular environments by using a comparative approach.

Editor: Miguel Olalla-Tárraga

APPENDIX 1 LITERATURE SOURCES USED IN COLLECTING PREDATOR RICHNESS AND LIZARD RICHNESS FOR ISLANDS SMALLER THAN 50,000 KM²

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