

A hump-shaped density–area relationship for island lizards

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We evaluated the density of *Anolis* lizards as a function of island area, habitat diversity, and topographic diversity on the Grenadines islands. We found a hump-shaped density–area relationship. Density at sea level increased with island area until an island was sufficiently large to contain multiple habitat types. Beyond this area threshold, average sea level density declined with island area. Increased species interactions on larger islands may explain the density decline.

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We examined how island area, and correlated attributes such as habitat and topographic diversity, influence *Anolis* lizard density. The species–area relationship (SAR) is often invoked to understand how area influences species richness (Rosenzweig 1995). This relationship, ecology’s closest approximate to a “law”, holds that species richness increases as a power-law function of area ($S \propto A^z$, where S is the number of species, A is island area, and z is the power-law exponent, Preston 1962, Lesser Antilles SARs: Losos 1996, Ricklefs and Lovette 1999).

Is there a similar law for the density of individuals? The density–area relationship (DAR, also referred to as the individuals–area relationship, Connor et al. 2000) is intrinsically linked to the SAR (Wright 1988, Matter 2000). Indeed, Preston (1962) assumed a constant total density of individuals and lognormal species–abundance distributions to provide a derivation of the SAR. The literature addressing the DAR is small relative to that addressing the SAR. Empirical studies from different systems report conflicting shapes of the DAR (Connor et al. 2000).

Two primary factors have hindered generalizing the relationship between the density of individuals and area. Firstly, the number of species within the studied guild has varied across the array of sites used to evaluate the

DAR (Diamond 1970, Jaenike 1978b, Wright 1980, Bengtson and Bloch 1983, Haila et al. 1983). Hence, density and species number covary, making detecting the DAR itself difficult (Gaston and Matter 2002). For topographically diverse islands, the only attempt to isolate area’s influence on density from changes in species richness was statistical and suggested that similar process govern the SAR and DAR (Nee and Cotgreave 2002). The simple *Anolis* lizard communities examined in this study allow the DAR to be analyzed without the confounding effects of covariation between density and species number.

Secondly, the DARs generated for islands and habitat patches have been considered together despite the different ecological processes operating in these two cases (Gaston and Matter 2002). Examinations of animal density in habitat patches tend to maintain a constant habitat type of variable size (Bender et al. 1998, Debinski and Holt 2000). Local populations residing within the patches tend to be connected by dispersal (Bowers and Matter 1997). On true islands, characteristics such as habitat diversity, topographic diversity, and maximum island elevation covary with island area. Colonization also varies between islands. Examining lizard density changes on true islands addresses how

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density changes in response to island characteristics and species interactions.

Three distinct hypotheses predict contrasting relationships between lizard density and island area (reviewed by Connor et al. 2000). Ecological theories, such as the equilibrium theory of island biogeography, were derived using the null assumption that the density of individuals remains constant (MacArthur and Wilson 1967). Island biogeography assumes that the density of individuals remains constant to attribute the SAR to changes in area per se. MacArthur and Wilson (1967) did not explicitly state whether the constant density assumption applies to individual species or groups of species. If the constant density is assumed to apply to groups of species, the density of each species on more speciose, larger islands must, on average, decline (Schoener 1986).

The resource–concentration hypothesis predicts that density will increase with increasing area. The hypothesis holds that density will increase as the diversity and concentration of resources in larger areas increases carrying capacities (Root 1973). The hypothesis was initially intended to explain the high insect density observed in resource-rich habitat patches and was based on the tendency of individuals to be attracted to and remain within large patches (Root 1973). However, it has since been more broadly interpreted to suggest that increases in the abundance and diversity of resources with area will increase the density of individuals (Connor et al. 2000).

The density–compensation hypothesis predicts that density will decrease with increasing area. Species are predicted to expand their ecological niches on small islands when released from competition and predation (MacArthur 1972). The potential for density compensation is greatest on small islands with few competitors and predators. The ability of a species to expand its ecological niche depends on habitat suitability (Diamond 1970, Case 1975, Lister 1976a, 1976b, Gaston et al. 1999). Anole density-compensation would be enabled by a release from predation by or competition with insectivorous birds.

We assessed the plausibility of these hypotheses for Grenadines anoles. We documented lizard density on thirteen Grenadines islands to investigate how the density of a single species varies with island area and its correlates (habitat and topographic diversity). This examination builds upon past research that debated the relative influence of competition and predation in regulating anole density in the West Indies (Wright 1981, Waide and Reagan 1983, Wright et al. 1984). Wright (1981) observed declining anole density with increasing area on a series of larger islands in the West Indies. The seven islands included in the study ranged in size from 4 to 8776 km². The thirteen islands included in this study range in size from 0.03 to 35 km². Our study islands have the advantage of having been a single

land mass during periods of lower sea level (Heatwole and Mackenzi 1967). Hence, extinction, rather than differential colonization, is the primary determinant of species occurrence on the study islands (Rand 1969, Losos 1996). Indeed, the occurrence of *Anolis* species on the islands is non-random with respect to island area and habitat diversity. All islands host the small anole, *A. aeneus*. The larger anole, *A. richardi*, is restricted to the largest two islands, which are at opposite extents of the Grenadines. The large island of Grenada, which is just south of the Grenadines, contains the only large and nearby potential source populations of both species (Roughgarden 1995). The Grenadines vary from small, low-elevation, and scrubby islands to larger, mountainous islands with complex forests and a variety of other habitats. Recently developed GIS based habitat and topographic maps enable more robust examinations of the influence of habitat and topographic diversity on island densities than previously possible (Bengtson and Bloch 1983, Haila et al. 1983). The Grenadines study system enables documenting a DAR for anoles while maintaining constant anole species richness and composition.

We plot the density of lizards at sea level to avoid confounding the density response to island area with that to other factors such as elevation (Roughgarden et al. 1983). Increasing island area may primarily append high-elevation, interior habitat that is less suitable for *A. aeneus*, which is thermally adapted to use warmer, open habitat (Schoener and Gorman 1968, Roughgarden et al. 1983). Solitary anoles exhibit a linear abundance decline with elevation (northern island: $r^2=0.90$, southern island: $r^2=0.73$; Buckley and Roughgarden 2005). Hence, increases in habitat diversity and elevation decrease island-wide density of the species (Gaston et al. 1999). By examining how sea level density changes, we maintain constant habitat and isolate the influence of island area and its correlates on density.

Methods

Island and site selection

We surveyed all accessible Grenadines islands that contained a substantial proportion of undisturbed habitat. We used topographic maps, digital elevation models, and remotely sensed images (Landsat TM) to identify both windward and leeward elevation gradients on each of the larger study islands. On the smaller islands, lizard abundance was surveyed in lizard habitat near sea level. Observations were conducted in July through August of 2004, which is within the wet season. We surveyed during hours of peak anole activity (between the hours of 1000 and 1600). Sites were distributed along the gradients and chosen to

contain a low abundance of cultivated plant species, relatively undisturbed habitat with a minimum of edge effects, and canopies less than approximately 10 m high. These properties maintained a constant ability to detect anoles across islands and elevations.

Anole abundance was estimated by the first author while pacing a 100 m linear transect for 2 h. This method allows greater geographic coverage than mark and recapture techniques (Diaz 1997). Repeat censuses of sites on other islands in subsequent years confirms the robustness (both relative and absolute abundance) of the censusing technique (Buckley and Roughgarden 2005). The 100 m transect was often along a low-use trail and chosen to be passable, representative, and to have little or no elevation change. If 100 m was traversed in less than two hours, an additional transect was surveyed adjacent to the initial transect.

Vegetation was scanned for anoles from the forest floor to canopy within 2 m on each side of transect. Upon observation of an anole, microclimate and perch height measurements were taken before resuming the survey. Estimates of abundance differences are conservative as more time was spent recording lizard data where lizards were more abundant. Elevation was estimated as the mean of GPS measurements at each end of the transect and confirmed with digital elevation models. A total of 36 sites were surveyed on 13 islands (9 sites among 7 “small” islands (<1 km²) and 27 sites among 6 “large” islands).

Habitat and topographic diversity

Data layers assembled in ArcGIS include a 90 m resolution digital elevation model (NASA Shuttle Radar Topography Mission) and a map of habitat types (Caribbean Vegetation Mapping Project, Areces et al. 1999). Island area was derived from a digital coastline map (NOAA shoreline data). The maximum elevation of each island was taken from the summit markers on topographic maps (1:25 000 scale). The habitat map was created using satellite images (Landsat Thematic Mapper) and empirical validation (Areces et al. 1999).

The map corresponds well to those by Stehle (1945) and Beard (1949) used in previous studies of habitat diversity in the Lesser Antilles (Ricklefs and Lovette 1999). The updated map uses a standard vegetation classification system developed for the Caribbean (Areces et al. 1999). The habitat designations for the study islands are dry woodlands, mangroves, xeric evergreen scrubland, littoral forest, and successional forest. Areas identified as urban were omitted when calculating habitat diversity and their relatively small area was subtracted from the total habitat area. For topographic diversity, we used ArcGIS to split all the terrestrial pixels

for the Grenadines islands into five elevation quantiles (0–9 m, 9–26 m, 26–54 m, 54–100 m and <100 m).

Habitat and topographic diversity were quantified using the inverse of Simpson's index, $1/\sum_{i=1}^n p_i^2$, where p_i is the proportion of the total area occupied by the i th of n vegetation types or elevation classes. Simpson's index, $\sum_{i=1}^n p_i^2$, represents the probability that any two randomly placed points will fall in a different habitat type or elevation class (Simpson 1949, Magurran 1988). The index is sensitive to evenness as it emphasizes habitat or elevation differences. This is appropriate as more even distributions of habitat types and elevation classes may enable habitat partitioning and greater species diversity. The inverse of Simpson's index ranges from one, when there is only one habitat or elevation class, to the total number of classes (n), when all classes occupy equal areas. The metric was applied previously to larger Lesser Antilles Islands by Ricklefs and Lovette (1999).

Statistical analysis

Analyses were performed using R (R Development Core Team 2004). Island area was log-transformed for all analyses. The maximum elevation, habitat diversity, and topographic diversity trends as a function of island area were fit using a linear regression model. For the DAR, we plot sea level densities to prevent confounding the influence of island area with that of maximum island elevation. The DAR data are intercepts and standard errors of regressions for islands on which there was a significant decline in abundance as a function of elevation and the regression accounted for at least 60% of the variation. Buckley and Roughgarden (2005) showed that the abundance of solitary anoles declines linearly with elevation. For the remaining islands, data are means and standard errors (when calculable).

An information-theoretic approach (minimum Akaike information criterion (AIC), Burnham and Anderson 2002) was used to stepwise fit a weighted multiple regression (quantile regression, R function `lm`). The AIC balances the likelihood of the model with model complexity. The regression was performed on the among-sites means or intercepts of lizard density for each island. Lizard density was estimated in fewer sites on the smaller islands. To account for this unequal certainty, the regression was weighted using the inverse of the variance. For islands where too few sites were surveyed to estimate variance, the maximum variance of all data points was assigned to the islands.

The stepwise model selection initiated with island area, habitat diversity, topographic diversity and the second order interactions between the effects. A polynomial fit was used for island area. The shape of the relationship was confirmed with splines and Loess

smoothing. The significance of the resultant model was compared to the null model (no effects) by analysis of variance. We report the correlation coefficient, F statistic, and two-tailed P-value for the entire model. For each term, we report the effect size, t statistic and two-tailed P-value. Effect sizes are indicated by η^2 , the ratio of effect sum of squares and total sum of squares.

Results

We first examine how maximum elevation, topographic diversity, and habitat diversity vary with island area. Maximum elevation ($r^2=0.86$; $F_{[1,11]}=67.74$; $P<0.001$) and topographic diversity ($r^2=0.91$; $F_{[1,11]}=107.95$; $P<0.001$) increase linearly as functions of (log-transformed) island area (Fig. 1a–b). Hence, maximum elevation and topographic diversity are correlates of area and their influences can not be separated from that of area in the DAR. In contrast, habitat diversity remains at 1 (a single habitat type) on islands with areas less than approximately 1 km². With increasing area on islands larger than approximately 1 km², habitat diversity increases (Fig. 1c). We can thus examine whether this area threshold for the increase in habitat diversity (1 km²) corresponds to changes in lizard density.

For the DAR, plotting *A. aeneus* abundance against island area yields a hump-shaped trend (Fig. 2). The apex of the hump occurs at the island area corresponding to the habitat diversity threshold (approximately 1 km²). For small islands below this threshold, the abundance of individuals increases approximately linearly with area. Above this threshold, *A. aeneus* density decreases with island area. The total lizard density on the largest two islands, the only two-species islands, is roughly equivalent to the highest single-species density (means \pm SE = 17.7 ± 0.33 and 24.2 ± 4.05).

The best fitting model predicts *A. aeneus* density as a polynomial function of island area and a linear function of topographic diversity and habitat diversity ($r^2=0.76$; $F_{[4,8]}=6.3$; $P<0.01$). The majority of the variance is accounted for by the significant second-order area term ($\eta^2=0.24$; $t_{[0.05,8]}=-3.76$; $P<0.006$) and the non-significant first-order area term ($\eta^2=0.39$; $t_{[0.05,8]}=1.20$; $P<0.3$). Habitat diversity ($\eta^2=0.077$; $t_{[0.05,8]}=2.33$; $P<0.05$) also has a significant effect, while topographic diversity has a non-significant effect ($\eta^2=0.076$; $t_{[0.05,8]}=2.18$; $P<0.06$).

The hump shape of the DAR is a robust finding. The fitted model is similar if we do not weight the stepwise regression ($r^2=0.76$; $F_{[4,8]}=6.3$; $P<0.014$). We also checked that the humped pattern is significant when excluding the densities on the two largest islands, where the abundance of each species may be depressed by partitioning density between the two-species. In this case, we did not weight the regression as only four

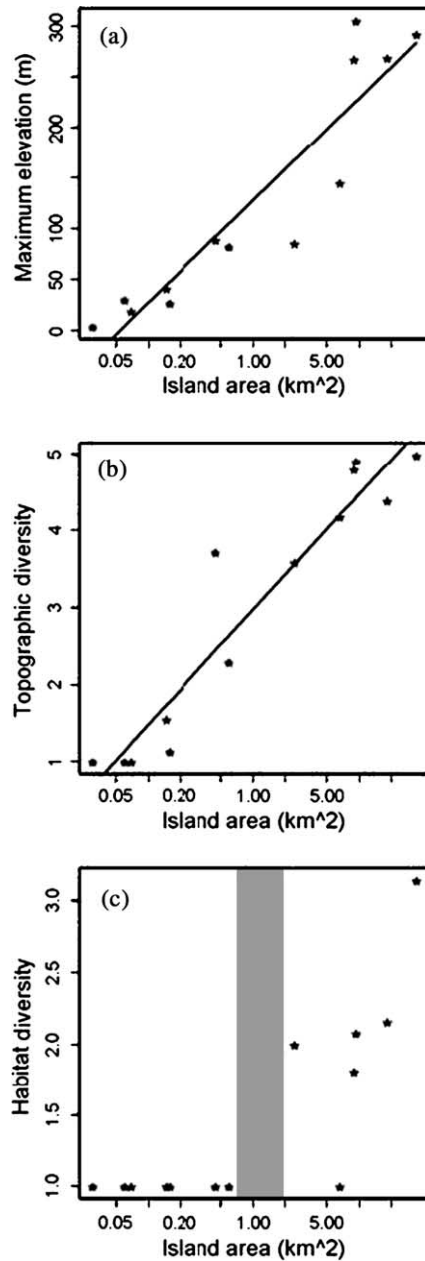


Fig. 1. (a) Maximum island elevation (m), (b) topographic diversity, and (c) habitat diversity as a function of elevation (m) on the Grenadines islands. The diversity metrics are calculated with the inverse of Simpson's index using habitat distribution maps and digital elevation models. Maximum island elevation and topographic diversity increase linearly with island area. Habitat diversity remains constant before increasing on the largest islands. Shading indicates the region of island area in which habitat diversity begins to increase.

estimates of variance remain when the two largest islands were removed. The resultant humped-shaped model predicts lizard density as a function of island area, topographic diversity, and habitat diversity ($r^2=$

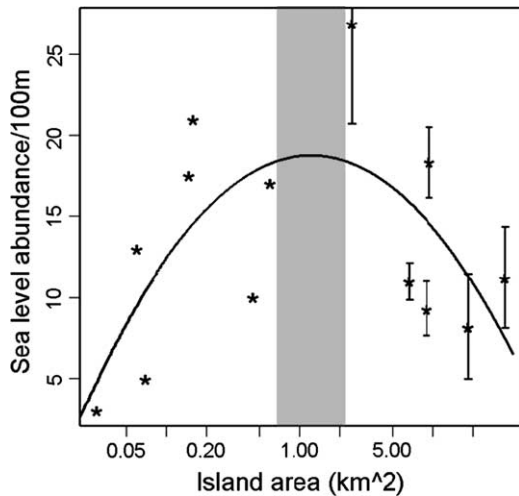


Fig. 2. Density–area relationship for *A. aeneus* on the Grenadines islands. Lizard abundances are sea level intercepts \pm SE of regressions for islands on which there was a significant decline in abundance with increasing elevation and the regression accounted for at least 60% of the variation. For the remaining islands, data are means \pm SE (when calculable). The DAR yields a hump-shaped pattern. The weighted polynomial regression was fit using area alone and does not reflect the fit of the multiple regression model. Shading indicates the region of island area in which habitat diversity begins to increase.

0.80; $F_{[4,6]}=6.0$; $P<0.03$). Analogous to the model including the two-species islands, the second-order area term ($\eta^2=0.15$; $t_{[0.05,6]}=-3.44$; $P<0.01$) and habitat diversity ($\eta^2=0.11$; $t_{[0.05,6]}=4.28$; $P<0.03$) are significant effects. The first-order area term ($\eta^2=0.37$; $t_{[0.05,6]}=1.76$; $P<0.1$) and topographic diversity ($\eta^2=0.07$; $t_{[0.05,6]}=2.65$; $P<0.07$) are non-significant effects.

Discussion

We have documented a hump-shaped DAR for the simple anole communities on the Grenadines islands. We now assess whether the predictions of each hypothesis correspond to the observed DAR. We do not observe the constant density with respect to island size assumed by island biogeography. Initially, lizard density increases with island area and the shift from low-elevation, scrubby islands to higher-elevation islands with complex forests. Increases in both the abundance and diversity of resources may be responsible for the increasing density, as predicted by the resource–concentration hypothesis (Root 1973). The threshold of island area at which density ceases increasing (approximately 1 km²) corresponds to the area at which islands begin to contain more than one habitat class. Increasing avian predation or competition with habitat diversity can account for this trend. A release from avian competition and predation yielding higher abundance on small islands

is consistent with the density-compensation hypothesis (MacArthur 1972).

Our findings demonstrate that spatial scale is an important determinant of DAR shape (Bowers and Matter 1997). On the smallest islands, factors including low genetic diversity, disturbance, and stochastic population fluctuations can reduce densities (Jaenike 1978b). Other studies have observed increases in population density until reaching a threshold island size. The threshold island size was similar to that corresponding to the peak of the DAR trend in this study (Jaenike 1978a, 1978b). Increases in the abundance and diversity of resources with island area increase lizard density until the islands are sufficiently large to harbor multiple habitat types.

Release from competitors or predators on small islands may enable density compensation (Diamond 1970, MacArthur 1972). Birds both prey on anoles (Wunderle 1981, McLaughlin and Roughgarden 1989) and compete for insect prey (Wright 1981). The richness of avian predators and competitors increases with both island area and habitat diversity in the Lesser Antilles (Ricklefs and Lovette 1999, Ricklefs and Bermingham 2002, 2004). The absence of high-elevation, interior habitat on the smaller islands may prevent the establishment of some bird species with forest affinities (Terborgh et al. 1978). However, birds' habitat niches may also expand on Lesser Antilles islands with low avian diversity (Terborgh et al. 1978). The insular extinction rates for birds are greater than those for anoles (Williams 1969, Ricklefs and Cox 1972, Terborgh and Faaborg 1973, Case 1975). This tends to release anoles from bird predation and competition on small islands. The occurrence of *Anolis* species forms a nested pattern in the wider Lesser Antilles and on the more specious islands in the Greater Antilles (Roughgarden 1989). Local extinction of bird and anole species is non-random as a function of both island area and habitat diversity.

Anole densities have been studied on both smaller (Schoener 1986) and larger (Wright 1981) islands than those in this study. Schoener (1986) observed decreasing densities with island area for both *Anolis* lizards and spiders on small (0.1 to 0.5 km²) islands in the Bahamas. The anole species richness and composition varied between islands. The low-elevation islands were formed by sedimentation and are primarily covered with scrubby vegetation. Avian predation pressure may be higher in the Bahamas due to high bird dispersal between the islands. Predation may be facilitated by the scrubby vegetation and lack of habitat diversity. Indeed, Schoener and Schoener (1978) documented greater mortality, which was attributed to predation, on larger islands. Release from competition and predation is potentially the dominant driver of the anole DARs in both the Bahamas and the Lesser Antilles. However, the spatial scale at which this release ceases may be smaller

in the Bahamas where birds may be efficient predators on small islands.

On larger islands in the West Indies (4 to 8776 km²), Wright (1981) documented decreasing anole density with increasing island size. Neither species richness nor composition was constant across the islands. The range of island areas over which he observed a declining DAR corresponds to the declining region of our hump-shaped trend. His reported densities are consistent with an extrapolation of our DAR. He observes densities of approximately 3 lizards per 100m² on his largest study island. A decreasing DAR was also observed for anoles on Panamanian Islands (Wright 1979). Wright attributed these trends to the strength of competition between insectivorous birds and lizards. Waide and Reagan (1983) argued that trends in predation accounted for the West Indian DARs. In response, Wright et al. (1984) tested whether predation pressures on anole were lesser on smaller Panamanian islands with fewer species of avian predators. They failed to find an inverse relationship between predation rate and island size, suggesting competition as the dominant driver of density trends. Interactions between predators may limit the effect of additional predators by altering the efficiency of prey consumption (Case et al. 1979).

The influence of avian predation on *Anolis* populations varies considerably between islands in the West Indies (McLaughlin and Roughgarden 1989). Avian predation has been shown to determine anole density on some islands (McLaughlin and Roughgarden 1989) and has been demonstrated on Grenada (Wunderle 1981). Anole mortality varies inversely with island size on small Bahamian islands (Schoener and Schoener 1978). They attributed this trend to release from avian predators. The strength of anole predation in the Grenadines is not yet known.

Resource limitation may regulate density more strongly than avian predation. Resource limitation has been demonstrated through experimental manipulations of the food supply on Grenada (Stamps and Tanaka 1981a, 1981b) and through comparative studies elsewhere in the West Indies (Andrews 1976, Pacala and Roughgarden 1985). Sympatric anoles throughout the Lesser Antilles exhibit consistent and substantial body size dimorphism. This suggests strong competitive pressure to reduce prey overlap (Schoener 1970).

The distinct DAR trend demonstrates that population sizes are non-random with respect to island size, topographic diversity and habitat diversity on the study islands. While we can not isolate the influence of topography from the effect of island area, the hump-shaped pattern suggests that neither is the exclusive determinant of the DAR. Habitat diversity is implicated as a driver of the DAR as the apex of the DAR corresponds to the incidence of habitat diversity. Sea level habitat is relatively constant as a function of island

size. The ability of an island with more habitat diversity to contain more predators and competitors is a potential means by which the habitat diversity influences anole density. The constancy of sea level habitats maintains an approximately constant ability to detect anoles. Maintaining constant species diversity and composition minimizes the potential for the hump-shaped DAR to be a sampling artifact. As anoles maintain territories several meters in diameter and perch at similar heights and microclimates throughout all habitat types (Schoener and Gorman 1968, Buckley and Roughgarden 2005), changes in local habitat use should not affect sea level density estimates. The hump-shaped DAR demonstrates that deterministic processes in addition to stochastic events, influence densities on the small study islands (Lomolino 2000).

Analyses of insular density–abundance trends have incited questioning whether the SAR derivation from species–abundance distributions applies to islands (Wright 1988). Within the Grenadines and other land bridge islands, differential extinction as a function of island area appears to be the primary determinant of the SAR (Rand 1969, Losos 1996). Anole density responds systematically to island area, but does not remain constant as assumed in the derivation of the SAR.

By using simple communities, we examined DARs without the confounding effects of changes in species richness or composition. The observed hump-shaped pattern suggests that spatial scale is an important determinant of the relationship between area and density. Density increases until an island becomes sufficiently large to harbor habitat diversity. Beyond this threshold, density decreases with increased species interactions on larger islands.

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