Environmental filtering underpins the island species–area relationship in a subtropical anthropogenic archipelago

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Title: Environmental filtering underpins the island species–area relationship in a subtropical anthropogenic archipelago

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Running Head: Environmental filtering and the ISAR

Abstract

1. Numerous mechanisms have been proposed to explain the island species-area relationship (ISAR), including the passive sampling effect, the habitat diversity effect, ecological drift and a group of mechanisms jointly termed environmental filtering (or abiotic selection process).

However, determining which of these hypotheses underpins the ISAR in a given system remains an open and controversial question, particularly with regards to the environmental filtering.

2. The effect of environmental filtering on the ISAR for woody plants was tested on 29 islands in a subtropical land-bridge archipelago. Island area had a significant effect on species richness, while isolation was not found to have an effect. After controlling for the passive sampling effect and habitat diversity using a systematic sampling design, we found that a positive ISAR remained.

3. After controlling for island area and isolation, species richness was significantly affected by environmental conditions (e.g. total phosphorus, soil depth and bulk density).

4. When a null model was used that randomly assigned individuals to islands from the regional pool, the difference between the observed and expected richness was greater for smaller islands relative to larger islands.

5. *Synthesis.* Our results point to an overlooked role of environmental filtering in driving the ISAR. Consequently, our study highlights the importance of considering deterministic process in future analyses of the ISAR.

Keywords: Colonization and extinction, environmental filtering, habitat fragmentation, island species–area relationship, passive sampling, selection process, species density

1. Introduction

The island species–area relationship (ISAR) describes the near-universally observed pattern whereby the number of species increases with the area of the island sampled (Whittaker & Fernández-Palacios, 2007; Rosenzweig, 1995; Matthews, Guilhaumon, Triantis, Borregaard, & Whittaker, 2016). A variety of hypotheses have been proposed to explain the ISAR. **First**, the passive sampling hypothesis states that the number of species increases with island area due to large islands randomly sampling more individuals, and thus accumulating more species, from a pool of colonists than small islands (Connor & McCoy, 1979; Burns, Berg, Bialynicka-Birula, Kratchmer, & Shortt, 2010). **Second**, the habitat diversity hypothesis is based on the idea that larger islands have greater habitat diversity, which enables a greater range of habitat specialists to exist on an island (Hortal, Triantis, Meiri, Thebault, & Sfenthourakis, 2009; Gaston & Blackburn, 2000, Bracewell, Clark, & Johnston, 2018). **Third**, based on the equilibrium theory of island biogeography (IBT) (MacArthur & Wilson, 1963, 1967), larger islands sustain larger populations of species which reduces the probability of stochastic extinction (also known as ecological drift, Gilbert & Levine, 2017; Vellend, 2016). **Fourth**, a range of hypotheses related to environmental filtering or abiotic selection process (i.e. deterministic fitness differences between individuals of different species linked to environmental conditions; discussed in more detail, below) have been proposed (Whittaker & Fernández-Palacios, 2007; Vellend, 2010, 2016).

Environmental filtering can be an important driver of local species extinctions, but is not considered by IBT (Laurance, 2008; Morrison, 2011). For example, only the species which are adapted to the present environmental conditions, and thus achieve high fitness, are able to successfully colonize an island, maintain a high abundance and thus avoid extinction (Chisholm, Fung, Chimalakonda, & O'Dwyer, 2016); conversely, species that are not adapted to the present

conditions on an island are unlikely to establish, or are unable to maintain high abundance and thus have a higher chance of extinction (Vellend et al., 2006; Morrison, 2011). Generally speaking, smaller islands are more affected by factors such as edge effects and resource limitation (Ewers & Didham, 2006). These differences in terms of the physical characteristics of islands and resource limitation between smaller and larger islands are expected to result in a greater loss of specialist species from smaller islands (Benchimol & Peres, 2015), e.g., resulting in fewer late-successional species on smaller islands (Liu et al., 2019). Therefore, this abiotic selection process is expected to result in reduced species richness on smaller islands (Vellend, 2010, 2016; Schrader, König, Moeljono, Pärtel, & Kreft, 2019). In this context, environmental filtering involves a variety of different mechanisms (e.g. the greater role of disturbance in regulating the diversity of smaller islands), which have individually been proposed as explanations for the ISAR (Whittaker & Fernández-Palacios, 2007; Rosenzweig, 1995; Morrison, 2011).

Distinguishing between these different mechanisms for a given empirical system remains an open and controversial question (Chase et al., 2019). This is particularly the case for the environmental filtering mechanisms (Phillips, Halley, Urbina-Cordona, & Purvis, 2018; Giladi, May, Ristow, Jeltsch, & Ziv, 2014; Burns et al., 2010; Kelly, Wilson, & Mark, 1989), as few studies have directly tested the effect of environmental filtering on the ISAR while controlling for other confounding factors (Whittaker & Fernández-Palacios, 2007; Rosenzweig, 1995; MacDonald, Anderson, Acorn, & Nielsen, 2018); although the concept has received increased theoretical interest in recent years (Vellend, 2016; Hattermann, Bernhardt-Romermann, Otte, & Eckstein, 2018).

Traditionally, the passive sampling effect has been tested by controlling either the number

of individuals sampled (i.e. rarefied species richness) or the sample area (i.e. species density) (Phillips et al., 2018; Giladi et al., 2014; Kelly et al., 1989). The effect of habitat diversity on the ISAR has also been tested by controlling for the number of habitats (Gaston & Blackburn, 2000, Rosenzweig, 1995; Kelly et al., 1989). In addition, studies have tried to control area *per se* to look at the effect of habitat diversity. For example, Ricklefs and Lovette (1999) found, using multivariate statistical analyses, that after controlling for area *per se*, different taxonomic groups differ in their responses to area and habitat diversity. However, few studies have directly controlled for habitat diversity in addition to the number of individuals sampled (i.e. rarefied species richness per unit area) (Phillips et al., 2018). This is problematic as, even when the same number of individuals are sampled, it is likely that a larger sampling area will result in greater habitat diversity / heterogeneity (Liu, Vellend, Wang, & Yu, 2018); inversely, when sampling area is kept constant but not the number of individuals, a sample with more individuals is likely to contain more species (Connor, Courtney, & Yoder, 2000). **As a result, it is necessary to control for the passive sampling effect and the effects of habitat diversity simultaneously when assessing the role of other ecological processes in driving the ISAR. Alternatively, the relative importance of all the various processes can be assessed in combination.**

According to the environmental filtering hypothesis, the species that are better adapted to the environmental conditions on an island are more abundant on that island, whereas species that are less adapted to conditions are less abundant or absent. It is expected that in most systems not all species in the regional pool will be adapted to the conditions on a given island (i.e. all species are not functionally equivalent, as assumed by neutral models and IBT). Therefore, islands will have fewer observed species than expected based on the total number of individuals that they support (Burns et al., 2010). If the environmental filtering does drive the ISAR in a given

archipelago, the increasing strength of abiotic selection with decreasing island area will result in an increased likelihood of extinction of less adapted species on smaller relative to larger islands (i.e. the selection process will be stronger on smaller islands) (Carnicer, Brotons, Sol, & de Cáceres, 2008; Gaston et al., 2000), and in particular the difference between the observed and expected species richness (based on the number of individuals) will be greater for smaller islands than for larger islands. Thus, this provides a further empirical test that can be undertaken to establish the importance of the environmental filtering in driving the ISAR.

In this study, we sampled woody plants on 29 islands of varying size in an artificial reservoir in China that was inundated in 1959. As all trees on the sampled islands are the result of secondary succession after the inundation (Liu et al., 2018; Wilson et al., 2016), we have the opportunity to test which mechanism(s) drives the ISAR of woody plants in this system, without having to account for a possible extinction debt (Jones, Bunnefeld, Jump, Peres, & Dent, 2016). Using these sampled data, we tested for the role of the environmental filtering, after controlling for the passive sampling effect and the habitat diversity effect, on the ISAR. We made the following predictions: (1) a significant ISAR will still be observed after controlling for the passive sampling effect and habitat diversity effect; (2) an island's species richness will be related to the environmental conditions present on the island (i.e. evidence of the environmental filtering will be observed); and (3) the observed number of species on an island will be less than that calculated through the random assignment of individuals (from the total pool of individuals across all islands) to the island.

2. Methods and materials

2.1 Study site

The Thousand Island Lake (TIL) is an artificial reservoir, ranging from 29°22' to 29°50' N and 118°34' to 119°15' E in Zhejiang Province, eastern China (Fig. 1). The lake was created in 1959 by the inundation of more than 1000 mountain hilltops following dam construction on the Xin'an River. Currently, most of these forested areas (~90%) are dominated by Masson pine (*Pinus massoniana*) in the canopy and broad-leaved plants in the sub-canopy and understory (e.g., *Loropetalum chinensei*, *Vaccinium carlesii*, and *Rhododendron simsii*) (Hu, Feeley, Wu, Xu & Yu, 2011; Yu, Hu, Feeley, Wu, & Ding, 2012).

2.2 Sampling method

We surveyed the woody plants with DBH ≥ 1 cm on 29 islands in 2014-2015. On the 20 smaller islands (area < 1 ha), the entire island was covered by 5 $\times$ 5 m squares, and we recorded the species name and the number of individuals of each species in each square (Fig.1). On the 9 larger islands (area >1 ha), we firstly set up 2-3 transects (the length of each transect depended on the island area and shape; see Fig. 1) which traversed the edge and interior habitat of an island. Each transect was then divided into 5 $\times$ 5 m squares (Fig. 1), where we recorded the species name and the number of individuals of each species in each square. In addition, in 2015 we measured 15 soil variables on each island. One sample or measurement was taken at the midpoint of three of the four 5 $\times$ 5 m squares within each 10 $\times$ 10 m area on small islands, and samples were taken at the midpoint of five of the sixteen 5 $\times$ 5 m subplots within each 20 $\times$ 20 m area on large islands (Liu et al., 2018). A subset of nine soil variables was chosen due to high multi-collinearity between the original 15 variables (tested using Variance Inflation Factors with a threshold of < 5): available phosphorus (AP, mg/kg), ammonium nitrogen (NH₄⁺-N, mg/kg), litter layer depth (LLD, cm), maximum water holding capacity (WHC, g/kg), relative potential moisture of the soil (RPM, %), soil bulk density (SD, g/cm³), total nitrate (TN, %), total

phosphorus (TP, mg/kg), and soil depth (SDEP, cm) (for detailed sampling information see Liu et al., 2018).

2.3 Testing for a passive sampling effect and the habitat diversity hypothesis

In our dataset, the smallest sampled island contained the minimum sampling area (175 m^2) and the minimum number of sampled individuals (128). Thus, we treated the 175 m^2 as the unit area in the following analyses. We also consider these to be a single habitat (i.e. controlling for habitat diversity) in this unit area due to its small size relative to the size of most woody plants (Liu et al., 2018). Hence, we were able to account for the effects of passive sampling and habitat diversity on the ISAR by controlling for the number of sampled individuals (128) and the sampling area (175 m^2) across islands. Across all of the sampled islands, if the number of species is found to increase with island area whilst controlling for the number of individuals (i.e. the rarefied species richness per island), we assume that other factors underpin the ISAR in our study system (or at least that the ISAR is not primarily caused by the passive sampling effect). Similarly, if the number of species per unit area (i.e. species density) increases with increasing island area, we assume that the ISAR is not primarily caused by habitat diversity (or at least that other factors are also important in driving the ISAR).

To control for any passive sampling effect and/or effect of habitat diversity, we first randomly selected the continuous sampling area (175 m^2) on each island as the unit area by randomly selecting seven adjacent $5 \times 5 \text{ m}$ squares until the sampling area (175 m^2) was reached. Second, using this set of $5 \times 5 \text{ m}$ squares, we randomly sampled 30 individuals in the selected unit area – the minimum number of individuals across all random selected unit areas – to calculate the number of species (i.e. rarefied species richness per unit area). As stated above, if

rarefied species richness per unit area is still found to increase with island area it implies that the ISAR must be caused, at least in part, by other processes, likely the selection process or ecological drift. The random sampling of 5×5 m squares and individuals was repeated 1000 times, and the mean and standard deviation of the rarefied species richness per island, species density and rarefied species richness per unit area of each island were calculated.

2.4 Testing the environmental filtering

According to IBT, island isolation is also predicted to drive variation in richness between islands, independently of island area (MacArthur & Wilson, 1967). To account for any effect of isolation on the observed ISAR in our dataset (e.g. if by chance all of the large islands are also the least isolated), we used a generalized linear model (GLM) with the Poisson family to test the effects of three island attributes (i.e. island area: A, distance to the mainland: MD, and distance to the nearest island: ND) on the observed number of island species. We also tested two additional isolation metrics (the proportion of land within 500m and 2500m buffers around each island) instead of MD and ND, but results were equivalent and these metrics are not discussed further. The adjusted R -squared (R^2_{adj}) value of the GLM was calculated using the “rsq” R package (Zhang, 2018). In a similar manner, standard linear models were used to test the effects of the three island attributes on i) mean rarefied species richness per island, ii) species density, iii) rarefied species richness per unit area, and iv) total abundance per unit area. Standard linear models were used rather than Poisson GLMs as these four response variables were not integer data. Multicollinearity between predictors was tested using variance inflation factors (< 5), and all response variables were found to be normally distributed using a Shapiro–Wilk test. All predictors were log-transformed to induce normality and scaled to have a mean of zero and standard deviation of one to enable comparison of the relative effects of island size and isolation

(i.e. the standardized regression coefficients) among the different models.

We then extracted the residuals from the above regression models that related the observed number of island species, the mean rarefied species richness per island, species density and rarefied species richness per unit area to island area and isolation (i.e. MD and ND). These residuals (which were normally distributed) were used as response variables in a set of standard linear multiple regression model selections. The predictors were the nine environmental variables. Model selection was undertaken using a backwards selection process and Akaike's information criterion corrected for small sample size (AICc) (Burnham & Anderson, 2002). This analysis allowed us to test whether any of the environmental variables affected observed and rarefied richness on islands after controlling for the effects of island area and isolation.

In order to evaluate any difference between the observed species richness on an island and the expected island richness based on the random sampling of individuals from the regional pool, we used a null model approach. For each island, we randomly sampled the observed total number of individuals on the island from the pool of all individuals in the archipelago (i.e. the sum of the individuals across the 29 islands) (Tello et al., 2015). According to this randomization algorithm, all individuals have the same probability of becoming part of any local assemblage (i.e. island), that is, it is assumed that all species can successfully colonize all islands. The randomization algorithm was run 999 times and, for each island, we compared the observed number of species (α_{obs}) with the mean number of species (α_{null}) calculated using the 999 null model iterations. We calculated the standardized effect size, i.e. $\text{SES} = (\alpha_{\text{obs}} - \alpha_{\text{null}}) / \text{SD}(\alpha_{\text{null}})$, as a measure of the magnitude and direction of the difference between the observed and the null richness values for each island (Gotelli & McCabe, 2002; Jung, Violle, Mondy, Hoffmann, & Muller, 2010). A positive SES value greater than 1.96 indicates that the observed number of

species on an island is significantly larger than the expected species richness based purely on the random assignment of individuals from the regional pool. In contrast, a negative SES value less than -1.96 represents an observed island richness value that is significantly lower than expected (i.e. approximate statistical significance at the 5% level for a two-tailed test). Thus, negative SES values indicate that islands have fewer species than expected based on the total number of individuals that they may support, and provide evidence supporting the role of the environmental filtering in driving the observed richness pattern in a given study system.

Except where stated otherwise, all analyses were conducted using R (version 3.1.2, R Core Team, 2017) and the vegan package (Oksanen et al., 2013).

3. Results

The observed species richness on the islands ranged from 8 to 50 species. The mean rarefied species richness per island ranged from 8 (SD: 0.00) to 21.93 (SD: 2.15). The mean species density (i.e. the number of species per 175 m²) ranged from 8 (SD: 0.00) to 18.33 (4.46), and the mean rarefied species per unit area ranged from 5.06 (0.82) to 9.79 (1.72) (Fig. 2). Significant correlations were observed between all pairs of observed species richness, mean rarefied species richness per island, and mean rarefied species richness per unit area (Spearman's $\rho > 0.64$ and $P < 0.001$ for all cases) (electronic supplementary material, Table S1).

For the three physical island attributes, island area rather than isolation (i.e. ND and MD) had the largest effect on observed species richness, rarefied species richness per island, species density, and rarefied species richness per unit area (Table 1); the effect was significant in each case (Table 1). When the number of individuals per unit area was used as the response variable, none of the predictors, or the model itself, were significant (Table 1). The observed number of

species significantly increased with increasing island area (Fig. 2a, $slope=4.42$, $R^2=0.70$, $P<0.001$), as did the rarefied species richness per island (Fig. 2b, $slope=1.03$, $R^2=0.43$, $P<0.001$), species density (Fig. 2c, $slope=0.80$, $R^2=0.33$, $P=0.001$) and the rarefied species richness per unit area (Fig. 2d, $slope=0.321$, $R^2=0.32$, $P=0.001$). There was no significant linear relationship between total abundance per unit area (i.e. the individual density) and island area (Fig. 3, $R^2=0.07$, $P=0.15$).

Total soil phosphorus, soil **bulk** density and soil depth significantly affected the residuals of observed species richness, rarefied species richness per island, species density, and rarefied species richness per unit area (Table 2), indicating that these environmental factors significantly affected island richness when area and isolation were controlled for.

For all islands, the observed species richness was less than the expected species richness when the number of individuals in each island's sample was kept constant (Fig. 4a). The standardized effect size (SES) values were all negative and were found to be significantly positively related to island area (Fig. 4b, $R^2=0.30$, $P=0.002$), which means that the difference between the observed and expected number of species was larger for smaller islands.

4. Discussion

Although a number of studies have found that the number of species (i.e. species richness) increases with island area (i.e. a positive ISAR) for multiple taxa in both TIL (Yu et al., 2012; Song, Holt, Si, Christman, & Ding, 2018) and other systems (Matthews, Guilhaumon et al., 2016), understanding of the exact mechanism(s) underpinning the ISAR **remains** limited (Whittaker & Fernández-Palacios, 2007; Chase et al., 2019). The results of the present study illustrate that, in our study system, the number of woody plants species still increases with area

even after controlling for the number of individuals and the diversity of habitats (Fig. 2). By accounting for both of these factors, we were able to minimize the effects of both passive sampling and habitat diversity (or habitat heterogeneity) (Liu et al., 2018) as drivers of the observed positive ISAR. This allowed us to undertake the first comprehensive test of the role of environmental filtering as a mechanism for the ISAR.

IBT postulates that the number of species on an island is dependent on both island isolation and area (MacArthur & Wilson, 1967). However, in our study island area was the main factor affecting the rarefied species richness per island, species density, and the rarefied species richness per unit area, whilst isolation (i.e. MD and ND) had no significant effect (Table 1). The lack of a significant effect of isolation observed here is consistent with other studies in land-bridge island archipelagos (Benchimol & Peres, 2015; Wilson et al., 2016; Yu et al., 2012) and indicates that isolation is not a primary variable driving community assembly in these systems, at least for certain taxa. One possible reason for this result is that these islands were isolated from the mainland only ~60 years ago, following inundation. All trees on the islands are thus the result of secondary succession, which likely reduces any effect of isolation. It may also be the case that the islands studied here are not that isolated in absolute terms for woody plants, that is, the degree of isolation may not pose too much of a barrier for plant dispersal.

When considering the relationship between island area and species diversity, a small number of previous studies have tested the relationship between species density and island area (e.g. Sfenthourakis & Panitsa, 2012). These studies have not reported a constant response of species density to habitat area (Kelly et al., 1989; Sfenthourakis & Panitsa, 2012), although one study (Giladi et al. 2014) found that species density was significantly positively correlated with habitat area at small spatial scales in a newly formed ecosystem; this is consistent with our

findings (Fig. 2b). However, high species density in larger areas may be also caused by a sampling effect, whereby more individuals may be included inside a standardized plot (Phillips et al., 2018). To eliminate this effect, we rarefied the species richness per unit area; following this we still found a positive relationship between rarefied species richness per unit area and island area (Fig. 2d). In contrast, the total abundance per unit area showed no significant linear relationship with island area (Fig. 3). We also found previously that the dissimilarity in species composition within islands showed no significant correlation with island area (Liu et al., 2018); this suggests that intra-island compositional heterogeneity does not play a role in driving the ISAR in this system (see Chase et al., 2019). Thus, again, these results indicate that the effects of both passive sampling and habitat diversity are not the only drivers of the ISAR in our study system. That is not to say that habitat diversity is not important at the whole island scale, but just that a positive ISAR remains even when habitat diversity is controlled for. As such, the positive ISAR we observed must be at least partly driven by other causes, such as either the environmental filtering or ecological drift, or a combination of these (MacArthur & Wilson, 1967; Hubbell, 2001; Whittaker & Fernández-Palacios, 2007; Vellend, 2016, 2010).

Some studies have suggested that random extinction via ecological drift is the most likely explanation for a positive ISAR, as the role of ecological drift is predicted to increase in importance with decreasing island area (Fukami, 2010; Hubbell, 2001). However, Liu et al. (2018) found that ecological drift did not explain differences in species composition between islands in TIL. In order to distinguish which of the two processes – environmental filtering versus drift – was a more important driver of the ISAR in our study system, we tested the extent to which a set of nine environmental variables could explain the different measures of richness when the effects of island area and isolation were controlled. Our results indicate that soil

variables, such as total phosphorus, soil **bulk** density and soil depth are significant determinants of species richness – species richness decreased with decreasing total phosphorus and soil depth, as well as with increasing soil **bulk** density (Table 2). These physical conditions (e.g. nutrient limitation, soil **bulk** density and depth) may limit which species can establish on islands, as only a small subset of species from the regional pool are able to successfully establish and persist (given the physical conditions present) in the long-term on islands (Laurance, 2008; Schrader et al., 2019). This result also provides further support for previous findings of the importance of phosphorus limitation in structuring subtropical forest ecosystems (Liu et al., 2014).

The environmental variables included here are not necessarily comprehensive, and it is likely that unmeasured abiotic or biotic variables also play important roles in filtering the species on these islands. For example, previous studies have shown that seed germination in small fragments is constrained due to edge effects (e.g. hotter, drier conditions and increased light penetration; Bruna, 1999), as well as an increased prevalence of seed predators (e.g. Mendes et al., 2016). In particular, edge-related forest disturbance (e.g. wind-throws) will increase tree mortality which, in turn, affects the species diversity on small islands (Benchimol & Peres, 2015).

The role of environmental filtering was further supported by our null model results which revealed that the observed number of species on islands, especially the smaller islands, was significantly lower than the expected number of species when the same number of individuals was sampled (Fig. 4). It should be noted that dispersal limitation, resulting in an aggregated distribution of individuals of the same species in space, should also generate a similar result. However, we further found that small islands were dominated by several of the same **native** species (e.g. *Rhododendron simsii*, *Loropetalum chinense*, *Pinus massoniana*) (electronic

supplementary material, Fig. S1; see also Hu et al., 2011); a similar finding has been reported for animal taxa in the TIL (Wang, Bao, Yu, Xu, & Ding, 2010). In addition, island isolation was not found to be a primary driver of species composition in this system (Liu et al., 2018). These findings suggest that, with the exception of these dominant species, which are dominant pioneer species in early successional subtropical forests, most woody plant species (i.e. the late-successional plant species) are prone to unsuccessful colonization on smaller islands (Liu et al., 2019). **In addition, due to the early succession stage of the forest on these islands, it is unlikely that an extinction debt is biasing any of the results found here.** As such, we would argue that our results provide strong evidence for the role of the abiotic selection process **or** environmental filtering **in driving the ISAR**, rather than dispersal limitation.

In sum, our study focused on distributional data of woody plant individuals on islands in the TIL and, by effectively controlling for variation in the effects of sampling and habitat diversity across islands, we have shown that the positive ISAR observed in this system is likely due, at least in part, to environmental filtering. Our results indicate that deterministic processes are important in structuring plant communities in land-bridge islands, and provide support for the role of environmental filtering or abiotic selection as a mechanism for the ISAR more generally.

Ethics. This study did not require ethical approval because no animals were handled.

Data accessibility. **The island attributes, species diversity and environmental variables on the studied islands can be obtained from the Dryad Digital Repository.**

Authors' contributions. JL and MY conceived the study; MY obtained the funding and

coordinated the study; JL, LZ and DW conducted field work. JL, TM and JJJL executed the statistical analysis; JL and TM wrote the first version of the manuscript. All authors gave final approval for publication.

Competing interests. We have no competing interests.

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Table 1 Generalized linear model (GLM) and simple linear regression results. For the GLM model fitting, the response variable was observed species richness, while for the multiple linear regression models the response variables were the mean rarefied species richness per island, species density, rarefied species richness per unit area, and total number of individuals per unit area. Island area (A), distance to mainland (MD), and distance to the nearest island (ND) were the explanatory variables in all cases. The significance of the standardized regression coefficients and the adjusted R -square (R^2_{adj}) values are also presented. Significance level: *** $P \leq 0.001$, ** $P \leq 0.01$.

	A	MD	ND	R^2_{adj}	F	P
Observed species richness	0.023***	0.007	0.002	0.556	22.134	<0.001
Rarefied species richness (per island)	0.663***	0.145	0.044	0.388	6.925	0.002
Species density	0.604***	0.209	-0.067	0.300	5.005	0.007
Rarefied species richness (per unit area)	0.582**	-0.008	-0.069	0.253	4.167	0.015
Number of individuals per unit area	0.337	0.268	-0.297	0.116	2.232	0.109

Table 2 Multiple linear regression model selection results. The response variable was the residuals from a regression model that relates observed and rarefied species richness to three island attributes. Nine environmental variables (available phosphorus, ammonium nitrogen, litter layer depth, maximum water holding capacity, relative potential moisture of the soil, soil bulk density, total nitrate, total phosphorus, and soil depth) were used as explanatory variables. Only the retained variables in the final regression model chosen using backwards selection are shown ($P < 0.05$).

	Estimate	Std. Error	<i>t</i> -value	Pr(> <i>t</i>)
Observed species richness				
Total phosphorus	0.009	0.003	2.638	0.014
Soil depth	0.096	0.037	2.601	0.016
Soil bulk density	-4.516	1.614	-2.798	0.010
Total Nitrogen	-8.856	3.978	-2.226	0.036
Rarefied species richness per island				
Total phosphorus	0.014	0.006	2.372	0.026
Soil depth	0.194	0.076	2.562	0.017
Soil bulk density	-12.980	4.340	-2.99	0.006
Species density				
Total phosphorus	0.015	0.005	2.907	0.007
Soil depth	0.139	0.061	2.285	0.031
Soil bulk density	-8.965	2.704	-3.316	0.003
Rarefied species richness per unit area				

Total phosphorus	0.005	0.002	2.239	0.022
Soil depth	0.070	0.031	2.252	0.034
Soil bulk density	-4.442	1.782	-2.492	0.020

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Figure Legends

Figure 1. The location of Thousand Island Lake and the sampling design employed. The lower left figure represents the placement of seven adjacent 5×5 m subplots, with a schematic representation of a hypothetical small island of ~0.14 ha (left) and a large island of ~1.33 ha (right). In the right hand figure, the red islands are those that were selected for sampling.

Figure 2 Relationships between alpha diversity (measured in four ways) and island area. (a) Observed number of species on islands; (b) rarefied species richness on each island (rarefied to 128 individuals for each island); (c) species density, calculated from repeated samples of a constant total contiguous plot area (175m²); and (d) rarefied species richness in each random selected contiguous plot (rarefied to the minimum number of individuals across all unit areas). Error bars around the data points show the standard error of the mean. The blue line is the best fit linear regression line and the grey area relates to the 95% confidence interval around the line. Point size is related to island area.

Figure 3 The relationship between the mean total abundance per unit area (i.e. 175 m²) and island area. The dotted line is the best fit linear regression line and the grey area relates to the 95% confidence interval around the line. Point size is related to island area.

Figure 4 The relationship between island area and (a) both the observed number of species (red points) and the mean expected number of species (black points) from the null model analysis; and (b) the standardized effect size between the observed and expected number of species. The error bars in (a) represent the 5th and 95th quantiles of the expected number of species when the number of individuals on each island were randomly sampled from the regional pool 999 times. The dotted line in (b) is the best fit linear regression line and the grey area relates to the 95% confidence interval around the line. Point size is related to island area.