

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

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1 **Research article: Journal of Ecology**

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

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16 **Running Head:** Environmental filtering and the ISAR

17

18

19 **Abstract**

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

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

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

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

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

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

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

41

42 1. Introduction

43 The island species–area relationship (ISAR) describes the near-universally observed pattern
44 whereby the number of species increases with the area of the island sampled (Whittaker &
45 Fernández-Palacios, 2007; Rosenzweig, 1995; Matthews, Guilhaumon, Triantis, Borregaard, &
46 Whittaker, 2016). A variety of hypotheses have been proposed to explain the ISAR. **First**, the
47 passive sampling hypothesis states that the number of species increases with island area due to
48 large islands randomly sampling more individuals, and thus accumulating more species, from a
49 pool of colonists than small islands (Connor & Mccoy, 1979; Burns, Berg, Bialynicka-Birula,
50 Kratchmer, & Shortt, 2010). **Second**, the habitat diversity hypothesis is based on the idea that
51 larger islands have greater habitat diversity, which enables a greater range of habitat specialists to
52 exist on an island (Hortal, Triantis, Meiri, Thebault, & Sfenthourakis, 2009; Gaston & Blackburn,
53 2000, Bracewell, Clark, & Johnston, 2018). **Third**, based on the equilibrium theory of island
54 biogeography (IBT) (MacArthur & Wilson, 1963, 1967), larger islands sustain larger populations
55 of species which reduces the probability of stochastic extinction (also known as ecological drift,
56 Gilbert & Levine, 2017; Vellend, 2016). **Fourth**, a range of hypotheses related to environmental
57 filtering or abiotic selection process (i.e. deterministic fitness differences between individuals of
58 different species linked to environmental conditions; discussed in more detail, below) have been
59 proposed (Whittaker & Fernández-Palacios, 2007; Vellend, 2010, 2016).

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

65 conditions on an island are unlikely to establish, or are unable to maintain high abundance and
66 thus have a higher chance of extinction (Vellend et al., 2006; Morrison, 2011). Generally
67 speaking, smaller islands are more affected by factors such as edge effects and resource
68 limitation (Ewers & Didham, 2006). These differences in terms of the physical characteristics of
69 islands and resource limitation between smaller and larger islands are expected to result in a
70 greater loss of specialist species from smaller islands (Benchimol & Peres, 2015), e.g., resulting
71 in fewer late-successional species on smaller islands (Liu et al., 2019). Therefore, this abiotic
72 selection process is expected to result in reduced species richness on smaller islands (Vellend,
73 2010, 2016; Schrader, König, Moeljono, Pärtel, & Kreft, 2019). In this context, environmental
74 filtering involves a variety of different mechanisms (e.g. the greater role of disturbance in
75 regulating the diversity of smaller islands), which have individually been proposed as
76 explanations for the ISAR (Whittaker & Fernández-Palacios, 2007; Rosenzweig, 1995; Morrison,
77 2011).

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

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

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

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

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

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

131 **2. Methods and materials**

132 **2.1 Study site**

133 The Thousand Island Lake (TIL) is an artificial reservoir, ranging from 29°22' to 29°50' N and
134 118°34' to 119°15' E in Zhejiang Province, eastern China (Fig. 1). The lake was created in 1959
135 by the inundation of more than 1000 **mountain hilltops** following dam construction on the Xin'an
136 River. Currently, most of these forested areas (~90%) are dominated by Masson pine (*Pinus*
137 *massoniana*) in the canopy and broad-leaved plants in the sub-canopy and understory (e.g.,
138 *Loropetalum chinensei*, *Vaccinium carlesii*, and *Rhododendron simsii*) (Hu, Feeley, Wu, Xu & Yu,
139 2011; Yu, Hu, Feeley, Wu, & Ding, 2012).

140 **2.2 Sampling method**

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

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

158 **2.3 Testing for a passive sampling effect and the habitat diversity hypothesis**

159 In our dataset, the smallest sampled island contained the minimum sampling area (175 m²) and
160 the minimum number of sampled individuals (128). Thus, we treated the 175 m² as the unit area
161 in the following analyses. We also consider these to be a single habitat (i.e. controlling for habitat
162 diversity) in this unit area due to its small size relative to the size of most woody plants (Liu et
163 al., 2018). Hence, we were able to account for the effects of passive sampling and habitat
164 diversity on the ISAR by controlling for the number of sampled individuals (128) and the
165 sampling area (175 m²) across islands. Across all of the sampled islands, if the number of species
166 is found to increase with island area whilst controlling for the number of individuals (i.e. the
167 rarefied species richness per island), we assume that other factors underpin the ISAR in our study
168 system (or at least that the ISAR is not primarily caused by the passive sampling effect).

169 Similarly, if the number of species per unit area (i.e. species density) increases with increasing
170 island area, we assume that the ISAR is not primarily caused by habitat diversity (or at least that
171 other factors are also important in driving the ISAR).

172 To control for any passive sampling effect and/or effect of habitat diversity, we first
173 randomly selected the continuous sampling area (175 m²) on each island as the unit area by
174 randomly selecting seven adjacent 5 × 5 m squares until the sampling area (175 m²) was reached.
175 Second, using this set of 5 × 5 m squares, we randomly sampled 30 individuals in the selected
176 unit area – the minimum number of individuals across all random selected unit areas – to
177 calculate the number of species (i.e. rarefied species richness per unit area). As stated above, if

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

183 **2.4 Testing the environmental filtering**

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

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

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

211 In order to evaluate any difference between the observed species richness on an island and
212 the expected island richness based on the random sampling of individuals from the regional pool,
213 we used a null model approach. For each island, we randomly sampled the observed total
214 number of individuals on the island from the pool of all individuals in the archipelago (i.e. the
215 sum of the individuals across the 29 islands) (Tello et al., 2015). According to this randomization
216 algorithm, all individuals have the same probability of becoming part of any local assemblage
217 (i.e. island), that is, it is assumed that all species can successfully colonize all islands. The
218 randomization algorithm was run 999 times and, for each island, we compared the observed
219 number of species (α_{obs}) with the mean number of species (α_{null}) calculated using the 999 null
220 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
221 measure of the magnitude and direction of the difference between the observed and the null
222 richness values for each island (Gotelli & McCabe, 2002; Jung, Violle, Mondy, Hoffmann, &
223 Muller, 2010). A positive SES value greater than 1.96 indicates that the observed number of

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

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

233 3. Results

234 The observed species richness on the islands ranged from 8 to 50 species. The mean rarefied
235 species richness per island ranged from 8 (SD: 0.00) to 21.93 (SD: 2.15). The mean species
236 density (i.e. the number of species per 175 m²) ranged from 8 (SD: 0.00) to 18.33 (4.46), and the
237 mean rarefied species per unit area ranged from 5.06 (0.82) to 9.79 (1.72) (Fig. 2). Significant
238 correlations were observed between all pairs of observed species richness, mean rarefied species
239 richness per island, and mean rarefied species richness per unit area (Spearman's rho > 0.64 and
240 $P < 0.001$ for all cases) (electronic supplementary material, Table S1).

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

246 species significantly increased with increasing island area (Fig. 2a, $slope=4.42$, $R^2=0.70$,
247 $P<0.001$), as did the rarefied species richness per island (Fig. 2b, $slope=1.03$, $R^2=0.43$, $P<0.001$),
248 species density (Fig. 2c, $slope=0.80$, $R^2=0.33$, $P=0.001$) and the rarefied species richness per unit
249 area (Fig. 2d, $slope=0.321$ $R^2=0.32$, $P=0.001$). There was no significant linear relationship
250 between total abundance per unit area (i.e. the individual density) and island area (Fig. 3,
251 $R^2=0.07$, $P=0.15$).

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

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

261 **4. Discussion**

262 Although a number of studies have found that the number of species (**i.e. species richness**)
263 increases with island area (i.e. a positive ISAR) for multiple taxa in both TIL (Yu et al., 2012;
264 Song, Holt, Si, Christman, & Ding, 2018) and other systems (Matthews, Guilhaumon et al.,
265 2016), understanding of the exact mechanism(s) underpinning the ISAR **remains** limited
266 (Whittaker & Fernández-Palacios, 2007; Chase et al., 2019). The results of the present study
267 illustrate that, in our study system, the number of woody plants species still increases with area

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

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

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

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

306 Some studies have suggested that random extinction via ecological drift is the most likely
307 explanation for a positive ISAR, as the role of ecological drift is predicted to increase in
308 importance with decreasing island area (Fukami, 2010; Hubbell, 2001). However, Liu et al.
309 (2018) found that ecological drift did not explain differences in species composition between
310 islands in TIL. In order to distinguish which of the two processes – environmental filtering
311 versus drift – was a more important driver of the ISAR in our study system, we tested the extent
312 to which a set of nine environmental variables could explain the different measures of richness
313 when the effects of island area and isolation were controlled. Our results indicate that soil

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

322 **The environmental variables included here are not necessarily comprehensive, and it is**
323 **likely that unmeasured abiotic or biotic variables also play important roles in filtering the species**
324 **on these islands. For example, previous studies have shown that seed germination in small**
325 **fragments is constrained due to edge effects (e.g. hotter, drier conditions and increased light**
326 **penetration; Bruna, 1999), as well as an increased prevalence of seed predators (e.g. Mendes et**
327 **al., 2016). In particular, edge-related forest disturbance (e.g. wind-throws) will increase tree**
328 **mortality which, in turn, affects the species diversity on small islands (Benchimol & Peres,**
329 **2015).**

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

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

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

353

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

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

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

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

361 **Competing interests.** We have no competing interests.

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367

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513
514

515 **Table 1** Generalized linear model (GLM) and simple linear regression results. For the GLM
 516 model fitting, the response variable was observed species richness, while for the multiple linear
 517 regression models the response variables were the mean rarefied species richness per island,
 518 species density, rarefied species richness per unit area, and total number of individuals per unit
 519 area. Island area (A), distance to mainland (MD), and distance to the nearest island (ND) were
 520 the explanatory variables in all cases. The significance of the standardized regression coefficients
 521 and the adjusted R^2 (R^2_{adj}) values are also presented. Significance level: *** $P \leq 0.001$, ** P
 522 ≤ 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

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526 **Table 2** Multiple linear regression model selection results. The response variable was the
 527 residuals from a regression model that relates observed and rarefied species richness to three island
 528 attributes. Nine environmental variables (available phosphorus, ammonium nitrogen, litter layer
 529 depth, maximum water holding capacity, relative potential moisture of the soil, soil bulk density,
 530 total nitrate, total phosphorus, and soil depth) were used as explanatory variables. Only the
 531 retained variables in the final regression model chosen using backwards selection are shown ($P <$
 532 0.05).

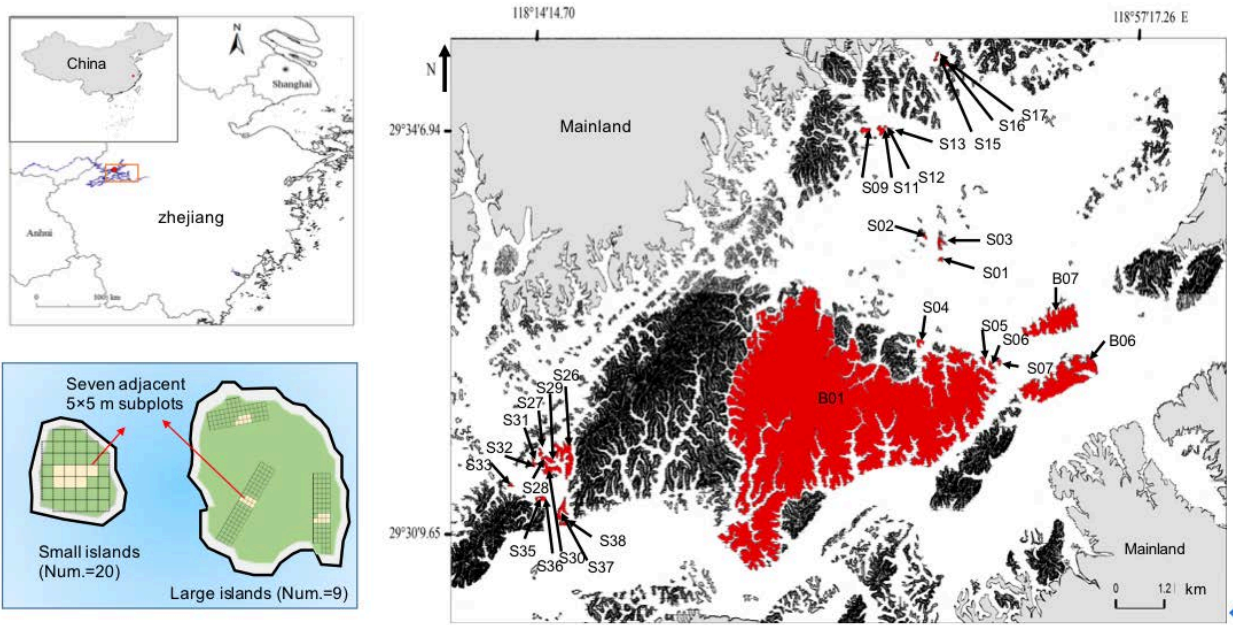
	Estimate	Std. Error	<i>t</i> -value	Pr(> <i>t</i>)
Observed species richness				
Total phosphorus	0.009	0.003	2.638	0.014
Soil depth	0.096	0.037	2.601	0.016
Soil bulk density	-4.516	1.614	-2.798	0.010
Total Nitrogen	-8.856	3.978	-2.226	0.036
Rarefied species richness per island				
Total phosphorus	0.014	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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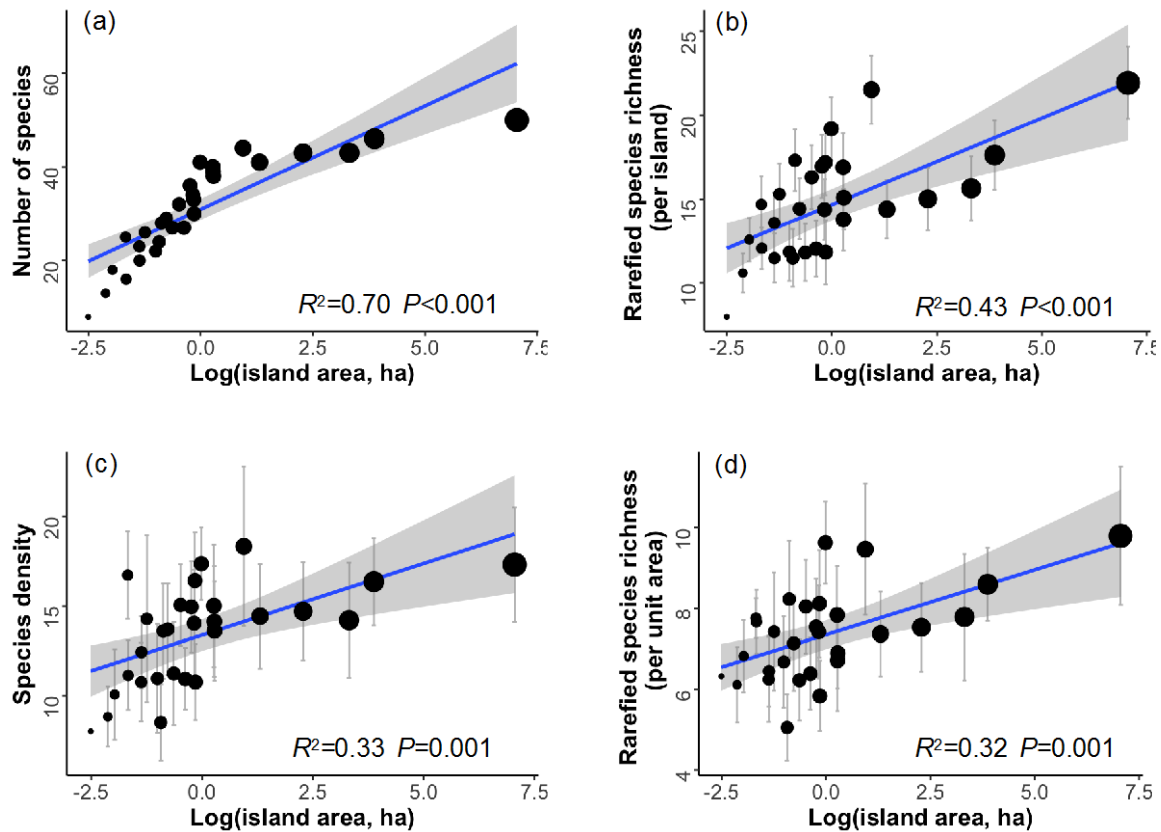
535 **Figure Legends**



536

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

541



542

543 **Figure 2 Relationships between alpha diversity (measured in four ways) and island area. (a)**

544 Observed number of species on islands; (b) rarefied species richness on each island (rarefied to

545 128 individuals for each island); (c) species density, calculated from repeated samples of a

546 constant total contiguous plot area (175m²); and (d) rarefied species richness in each random

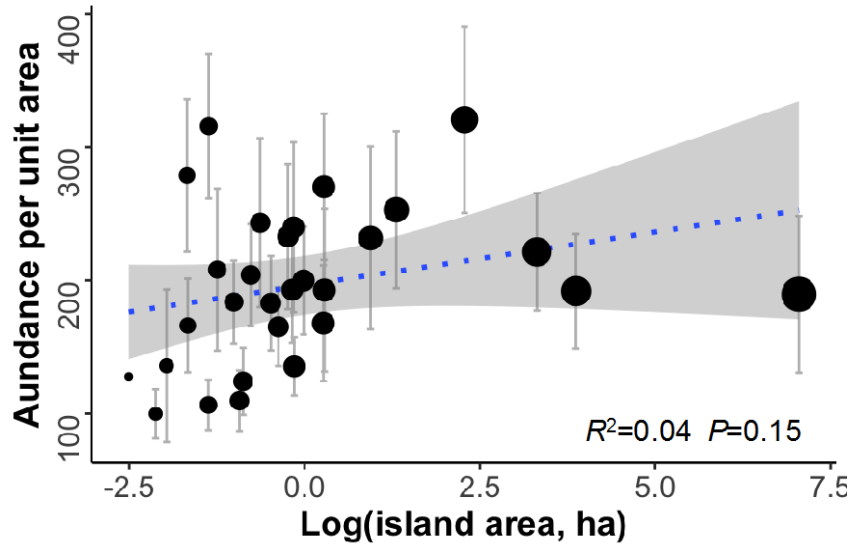
547 selected contiguous plot (rarefied to the minimum number of individuals across all unit areas).

548 Error bars around the data points show the standard error of the mean. The blue line is the best fit

549 linear regression line and the grey area relates to the 95% confidence interval around the line.

550 Point size is related to island area.

551

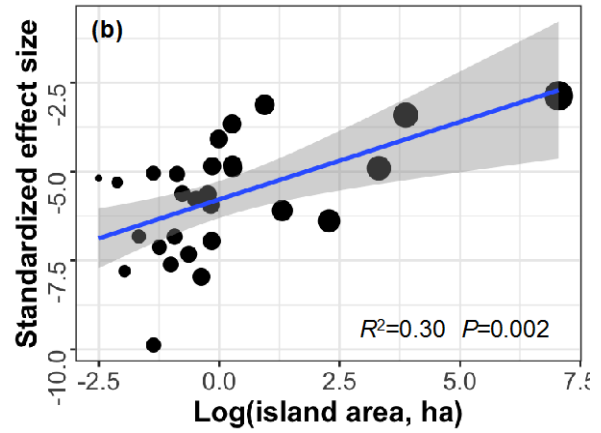
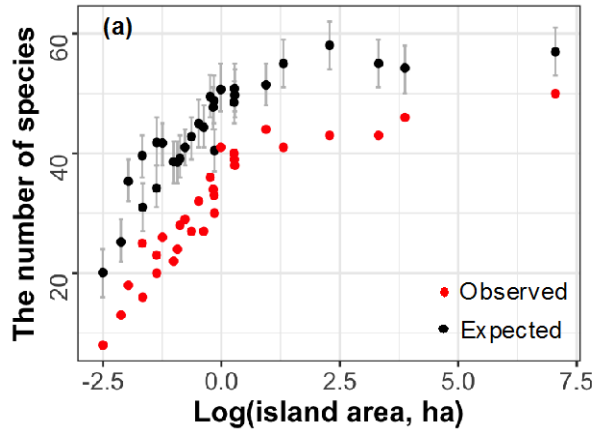


552

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

556

557



558

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

566