

1           **Article: Beta diversity patterns derived from island biogeography theory**

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16 **Abstract**

17 The Theory of Island Biogeography (TIB) has been successful in predicting alpha  
18 diversity patterns such as species-area relationships and species-abundance  
19 distributions. Although beta diversity (i.e. the dissimilarity of community composition)  
20 has long been recognized as an important element of the TIB and is crucial for  
21 understanding community assembly processes, it has never been formally  
22 incorporated into the theory. Here we derive theoretical predictions for the expected  
23 pairwise beta diversity values under a species-level neutral scenario where all species  
24 have equal colonization and extinction rates. We test these predictions for the avian  
25 community composition of 42 islands (and 93 species) in the Thousand Island Lake,  
26 China. We find that alpha diversity patterns alone do not distinguish a species-level  
27 neutral model from a non-neutral model. In contrast, beta diversity patterns clearly  
28 reject a species-level neutral model. We suggest that the presented theoretical  
29 integration beta diversity offers a powerful path for testing the presence of neutral  
30 processes in ecology and biogeography.

31

32 **Keywords:** neutral theory; null model; beta diversity; meta-community; incidence  
33 function; community assembly; regional species pool

## 34 INTRODUCTION

35 Island biogeography is undergoing a renaissance (Warren et al. 2015; Santos et al.  
36 2016; Patiño et al. 2017), at the heart of which lies the equilibrium theory of island  
37 biogeography (TIB) formulated by MacArthur and Wilson 50 years ago (1967). The  
38 TIB is most celebrated for elegantly linking species richness with colonization and  
39 extinction rates, which in turn are influenced by island area and distance to the  
40 mainland. Equilibrium TIB makes two key predictions: 1) equilibrium species  
41 richness depends on colonization and extinction rates; 2) community composition of  
42 an island is undergoing constant turnover when at equilibrium. While early empirical  
43 studies have focused on testing the equilibrium and temporal turnover predictions  
44 (Diamond 1969; Simberloff 1969; Simberloff and Wilson 1969, 1970; Diamond and  
45 May 1977), recent interest in TIB is stimulated by the success of Hubbell's unified  
46 neutral theory (a descendant of the TIB; Hubbell 2001), the advance of food web  
47 theories (Holt 2009), the developments of phylogenetic analyses (Valente et al. 2015;  
48 Lim and Marshall 2017), and the accumulation of island datasets (Weigelt et al. 2013,  
49 2016). Motivated by the desire for a general island biogeography theory, more and  
50 more complexities have been added to the original framework, including allometric  
51 scaling (Jacquet et al. 2017), trophic interactions (Gravel et al. 2011; Cazelles et al.  
52 2016), speciation (Chen and He 2009; Rosindell and Phillimore 2011; Rosindell and  
53 Harmon 2013), habitat heterogeneity (Kadmon and Allouche 2007), and island  
54 ontogenies (Whittaker et al. 2008; Borregaard et al. 2016). While the complexity of

55 the theory has increased, examinations to date have focused on alpha diversity  
56 patterns such as species richness (MacArthur and Wilson 1967), species-abundance  
57 relationships (Rosindell and Phillimore 2011; Rosindell and Harmon 2013; Kessler  
58 and Shnerb 2015), functional diversity (Jacquet et al. 2017), and endemism (Chen and  
59 He 2009).

60 One particular omission in the theory and tests of the TIB to date is beta diversity,  
61 i.e. the compositional dissimilarities among communities, a widely used metric in  
62 biodiversity studies (Leprieur et al. 2011; Stegen et al. 2013; Segre et al. 2014; Si et al.  
63 2016). The integration of beta diversity patterns into the TIB has the potential to  
64 unlock a range of uses in community assembly studies and the development of a  
65 unified meta-community theory (Leibold et al. 2004).

66

67 The concept of beta diversity was first introduced by Whittaker (1960, 1965) and  
68 was quickly linked to an array of important mechanisms in community assembly:  
69 biotic interaction (Graham and Fine 2008), environment filtering (Veech and Crist  
70 2007; Buckley and Jetz 2008), dispersal limitation (Ojima and Jiang 2017; Wu et al.  
71 2017), and historical contingency (Fukami and Nakajima 2011). However, despite the  
72 widespread recognition of the beta diversity concept, there is little consensus about  
73 the best way to measure it (Tuomisto 2010*a*, 2010*b*; Anderson et al. 2011).  
74 Depending on the purpose of a study, beta diversity could be measured as turnover  
75 (directional) or variation (non-directional) of compositional similarity (Nekola and

76 White 1999; Legendre and De Cáceres 2013); based on pairwise or multiple-sites  
77 comparisons (Hui and McGeoch 2014; Arita 2017; Latombe et al. 2017; Marion et al.  
78 2017); decomposed in additive or multiplicative framework (with respect to alpha and  
79 gamma diversity; Jost 2007; Cabral *et al.* 2014); calculated by incidence  
80 (presence-absence) or abundance data (Chao et al. 2016). Even for the commonly  
81 used pairwise beta diversity, there is a heated debate about what is the best way to  
82 partition it into richness difference and replacement (or nestedness and turnover)  
83 components (Baselga 2010; Podani and Schmera 2011; Legendre 2014; Baselga and  
84 Leprieur 2015). It is generally agreed that different measures quantify different  
85 aspects of communities and that their use should be guided by the question asked  
86 (Anderson et al. 2011; Legendre 2014). Although beta-diversity measures have been  
87 increasingly synthesized under more general frameworks such as Hill's number and  
88 variance of community matrix (Chao et al. 2016), only a few of them have been  
89 examined analytically from process-based theories (Chave and Leigh 2002; Condit et  
90 al. 2002; Zillio et al. 2005; Connolly et al. 2017). Moreover, theoretical  
91 considerations of beta-diversity patterns to date have been abundance-based and  
92 hence limited to more restricted datasets, such as vegetation plots (Chave and Leigh  
93 2002; Condit et al. 2002; Zillio et al. 2005). In summary, the link between beta  
94 diversity patterns and fundamental processes such as colonization and extinction in  
95 the TIB remain ill developed.

96

97 In this study, we set out to address this shortcoming and provide a theoretical and  
98 example empirical integration of beta diversity into TIB. Specifically, we present the  
99 first theoretical predictions for the expected pairwise beta diversity patterns for both  
100 Jaccard and Sørensen indices in the classic MacArthur and Wilson framework. This  
101 framework constitutes in essence a species-level neutral model (as opposed to the  
102 individual-level neutral theory; Hubbell 2009; Rosindell and Phillimore 2011). The  
103 species-level neutral model assumes that all species have the same colonization and  
104 extinction rates, while the individual-level neutral model assumes that all individuals  
105 have the same colonization and extinction rates, which allows species-level  
106 asymmetry to arise because of different abundance (Rosindell and Harmon 2013). We  
107 first derived the probability mass function and expected value of pairwise beta  
108 diversity in a general case where the equilibrium assumption is not required. We then  
109 examined our results under the classic MacArthur-Wilson equilibrium framework.  
110 Finally, we test the derived predictions for a dataset of 93 avian species occurring  
111 across 42 islands of the Thousand Island Lake Region in China (Appendix, Wang *et*  
112 *al.* 2010).

113

## 114 **MATERIAL AND METHODS**

115 To derive expected beta diversity, we need to consider the joint statistical distribution  
116 of multiple islands. We here focus on pairwise community comparisons, because  
117 average pairwise dissimilarity is shown to be the only unbiased and consistent

118 estimator when applied to empirical data (Marion et al. 2017). We also calculated the  
119 expected value of the partitioned components of pairwise beta dissimilarity for both  
120 Baselga and Podani families (Baselga 2010; Podani and Schmera 2011). To test our  
121 predictions, we applied an “Incidence Function” approach pioneered by Diamond  
122 (1975) and used by Connor and Simberloff (1978, 1979) during early debates of null  
123 models.

124

### 125 **Probability mass function of pairwise beta diversity**

126 All pairwise beta diversity indices share the same probability mass function to  
127 describe island community composition because they are calculated from four  
128 quantities: the total number of species of two islands  $N$  (regional species richness), the  
129 number of species shared by both islands  $k$ , the number of species unique to the first  
130 island  $i$ , and the number of species unique to the second island  $j$  (thus  $N = k + i + j$ ).  
131 Then the number of species present on the first island is  $i+k$ , and the number of  
132 species present on the second island is  $j+k$ .

133 Denoting the size of the mainland species pool as  $M$ , the probability mass function of  
134 pairwise beta diversity, conditioning on  $N$ ,  $k$  and  $i$ , can be derived as follows: let the  
135 occurrence probability of the  $i^{\text{th}}$  species on the first island be  $p$ , and the  $j^{\text{th}}$  species on  
136 the second island be  $q$ . Furthermore, assuming that the occurrence probabilities are  
137 properties of the island rather than of species, the probability of obtaining exactly  $i$   
138 unique species and  $k$  shared species from a regional pool of size  $M$  is given by

139  $p^{k+i}(1-p)^{M-(k+i)}$ . Similarly, the probability of obtaining  $j$  unique and  $k$  shared species on  
140 the second island is  $q^{k+j}(1-q)^{M-(k+j)}$ , which yields the probability of obtaining the  
141 regional community specified by  $i, j, k$  and  $M$ , as  $p^{k+i}(1-p)^{M-(k+i)}q^{k+j}(1-q)^{M-(k+j)}$ .

142 Assuming that species are neutral with respect to their occurrence probabilities  
143 within an island, we then count how many different combinations of island  
144 communities could be obtained with regional richness  $N$ ,  $k$  shared species, and  $i$   
145 unique species to the first island (the number of unique species to the second island is  
146 then fixed as  $k-i$ ). There are exactly  $\binom{M}{N}$  ways of choosing  $N$  out of  $M$  species to be  
147 present in either or both islands from the mainland species pool. Similarly, there are  
148  $\binom{N}{k}$  ways to choose  $k$  out of  $N$  species to be shared by both islands and for the unique  
149  $N-k$  species, there are  $\binom{N-k}{i}$  ways of assigning  $i$  species to the first island. After  
150 simplification, the probability of pairwise beta diversity conditioning on the total  
151 number of species of both islands  $N$ , the number of species shared by both islands  $k$ ,  
152 and the number of species unique to the first island  $i$  is:

$$153 \Pr(\text{regional community} \mid N, k, i) = \binom{M}{N} \binom{N}{k, i} p^{k+i} q^{k+j} (1-p)^{M-(k+i)} (1-q)^{M-(k+j)}$$

154 (1)

155

156 Because beta diversity measures (e.g. Jaccard and Sørensen indices) are usually  
157 undefined when  $N = 0$ , the expected pairwise beta diversity should be normalized by  
158 the term  $1 - (1-p)^M(1-q)^M$  to exclude “double-absence” scenarios (Anderson et al.  
159 2011). Only the expected Jaccard dissimilarity (Jaccard dissimilarity is defined as



160  $1 - \frac{k}{N}$ ) has a simple analytical form that is independent of the size of mainland  
161 species pool  $M$  (see Appendix S1 in Supporting Information for derivation; we do not  
162 show the analytical form of the expected Sørensen dissimilarity because the specific  
163 form depends on the size of mainland species pool):

$$164 \quad E(\text{Jaccard.dissimilarity}) = \frac{p+q-2pq}{p+q-pq} \quad (2)$$

165

166 It has a form that is similar to the expected pairwise Jaccard derived by Chase *et al.*  
167 (2011) but allows two islands to have different occurrence probabilities.  $p$  and  $q$  could  
168 also be interpreted as probabilities of the same island at different times, and in that  
169 case (2) becomes the expected temporal Jaccard dissimilarity. This quantity does not  
170 require any equilibrium assumptions of alpha diversity and hence could be seen as a  
171 generalized version of the apparent turnover derived by Diamond and May (1977)  
172 which is essentially a pairwise Sørensen dissimilarity index in equilibrium (Morrison  
173 2017).

174 We also calculated the expected pairwise beta diversity for Jaccard and Sørensen  
175 families as well as their partitioned components (for detailed formulas of the Baselga  
176 and Podani families see Baselga & Leprieur 2015) conditioning on both islands  
177 having species ( $i+k > 0$  and  $j+k > 0$ ) because empty islands are sometimes excluded  
178 from analysis (Wang et al. 2016). In Baselga's family, pairwise dissimilarity is  
179 partitioned into the nestedness component and the turnover component. The  
180 nestedness component measures the extent to which species in a smaller community

181 are a subset of species in a larger community, while the turnover component measures  
182 how much of the dissimilarity is caused by species replacement (Baselga 2010). The  
183 turnover component and the nestedness component in Baselga's family, respectively,  
184 correspond to the replacement component and the richness difference component in  
185 Podani's family (Legendre 2014).

186

### 187 **Island biogeography theory**

188 Following the stochastic version of the TIB (MacArthur and Wilson 1967), the  
189 occurrence probability of a species on an island is a function of colonization rate  $c$   
190 and extinction rate  $e$ :

$$191 \quad \frac{dp}{dt} = c(1-p) - ep \quad (3)$$

192 When occurrence probability of a species is at stochastic equilibrium (stationary  
193 distribution), the occurrence probability is:

$$194 \quad p_{i,eq} = \frac{c}{c+e} \quad (4)$$

195 Let  $\theta = \frac{e}{c}$ , which is the relative extinction rates, equation (4) becomes:

$$196 \quad p_{i,eq} = \frac{1}{1+\theta} \quad (5)$$

197 Substitute  $p = q = \frac{1}{1+\theta}$  into equation (2), the expected Jaccard dissimilarity when  
198 two islands have equal colonization and extinction probabilities is:

$$199 \quad E(\text{Jaccard.dissimilarity}) = \frac{2\theta}{1+2\theta} \quad (6)$$

200 To take into account asymmetry between islands (e.g. the effect of area, isolation or

201 habitat types), let  $p = \frac{1}{1+\theta}$  and  $q = \frac{1}{1+z\theta}$ , so that the relative extinction rate on the

202 second island is  $z$  times the relative extinction rate on the first island. Equation (2)

203 becomes:

$$204 \quad E(\text{Jaccard.dissimilarity}) = \frac{(1+z)\theta}{1+(1+z)\theta} \quad (7)$$

205

## 206 **Empirical tests**

### 207 **Data**

208 We use a published dataset of avian community composition for 93 birds and 42  
209 islands in The Thousand Island Lake, China to test our predictions (see Appendix in  
210 Wang *et al.* 2010). The region (29°22" – 29°50" N, 118°34"– 119°15" E) consists of  
211 an inundated lake with more than 1000 islands created by dam constructions in 1959.  
212 Because the islands were formed recently, there was no in situ speciation in this  
213 region. The relative small area of the region (573 km<sup>2</sup>) ensures that the islands are  
214 accessible to most of the bird species (Si et al. 2016). Bird occupancies from 2006 to  
215 2009 on 42 islands were documented using line-transect method. Island variables  
216 measured in the dataset include area, distance to mainland, habitat diversity and plant  
217 species richness.

218

### 219 **Incidence function and statistical analysis**

220 Because extinction rates and colonization rates are difficult to measure directly, an  
221 alternative way is to use an "Incidence function" approach to estimate parameters  
222 from a snapshot of occupancy patterns (Diamond 1975; Hanski 2009). To test the

223 predictions of island biogeography theory, equation (4) is modeled as a function of  
224 isolation and area. Parameters are fitted by maximum likelihood with binomial  
225 distribution. Three neutral models and one non-neutral model are examined in this  
226 study:

227 Neutral model 1: Inverse ratio

228 Colonization rates are modeled as an inverse ratio function of isolation:  $c = \frac{a}{I}$ , and  
229 extinction rates are modeled as an inverse ratio of area:  $e = \frac{b}{A}$ .  $a$  and  $b$  are fitted  
230 parameters.

231 Neutral model 2: Exponential

232 Colonization rates are modeled as an exponential function of isolation:  
233  $c = \exp(-aI)$ , and extinction rates are modeled as an exponential function of area:  
234  $e = \exp(-bA)$ .  $a$  and  $b$  are fitted parameters. Substitute  $c = \exp(-aI)$  and  
235  $e = \exp(-bA)$  into equation (4), the occurrence probability becomes

236 
$$p = \frac{1}{1 + \exp(-bA + aI)}$$
. Thus the exponential neutral model is equivalent to a logistic

237 regression without intercepts, which could be directly fitted by ‘glm’ in R with  
238 binomial distribution and logit link.

239 Neutral model 3: GLM

240 This model adds habitat diversity and plant richness to the predictors in addition to  
241 area and isolation in Neutral Model 2. AIC is used to select the best model. Area and  
242 isolation are log-transformed to ensure better linearity.

243 Non-neutral model: Aggregate species-level GLM

244 To take into account species-level non-neutrality, species identity is included as a  
245 fixed effect categorical variable in the GLM, which allows each species to have a  
246 different intercept (baseline occurrence probability) but share the same response to  
247 island area, isolation, plant richness and habitat types. This is essentially a stacked  
248 species distribution modeling approach (Calabrese et al. 2014; Ko et al. 2016), which  
249 increases the number of parameters by the number of species minus one (92  
250 parameters in this case). This procedure aims to capture the observed  
251 presence-absence variation among species but does not pin down the causes of  
252 species-level non-neutrality such as traits and abundance differences. More realistic  
253 assumptions of non-neutrality such as different responses to area and isolation could  
254 be made but are not the main focus of this paper. AUC and AIC values are calculated  
255 to compare the overall performance of the models. AUC is calculated with a  
256 Mann-Whitney U statistic using R package ‘PresenceAbsence’. AIC is calculated  
257 from the best-fitted likelihood function.  $\Delta AIC$  are calculated by subtracting the AIC  
258 of the null model (GLM with only one intercept) from the AIC of the fitted model.

259

## 260 **Predictions of alpha diversity and beta diversity**

261 The predicted species richness of each island is given by the summed fitted  
262 occurrence probabilities of all species as used in conventional stacked species  
263 distribution modeling (Calabrese et al. 2014; Ko et al. 2016). While predicted  
264 pairwise Jaccard dissimilarity can be calculated analytically from equation (2), the

265 partitioned nestedness and turnover components can only be estimated by simulations  
266 (we only present the results of Baselga's family because its partitioned components  
267 are independent with each other when gamma diversity is fixed; Baselga & Leprieur  
268 2015). We therefore estimate predicted pairwise beta diversity as the mean of 1000  
269 community matrices simulated from the fitted occurrence probabilities. Observed  
270 values are regressed against predicted values using ordinary least square.  $R^2$  is used as  
271 a measure of predictive power for alpha and beta diversity patterns. If the model  
272 predicts the observed patterns well, the fitted regression line should be close to the 1:1  
273 ratio line when observed values are plotted against predicted values. All statistical  
274 analyses are performed in R 3.3.2.

275

## 276 **RESULTS**

### 277 **Symmetric islands (same colonization and extinction rates for both islands)**

278 The expected Jaccard dissimilarity conditional on both islands having non-zero  
279 species richness increases monotonically with relative extinction rate  $\theta$  and the size  
280 (number of species) of the mainland species pool  $M$ . As  $M$  increases, the expected  
281 Jaccard dissimilarity converges to  $\frac{2\theta}{1+2\theta}$  (Fig. 1a). When decomposed into turnover  
282 and nestedness (or replacement and richness difference) components, contrasting  
283 patterns are observed: while the turnover component and the replacement component  
284 increase monotonically with  $\theta$  and  $M$  (Fig. 1b, e), the nestedness component and  
285 richness difference component are both unimodal functions of  $\theta$  with maximum

286 values less than 0.3 (Fig. 1c, f). The maximum nestedness decreases as  $M$  increases  
287 (Fig. 1c), while the maximum richness difference changes little with the increase of  $M$   
288 (Fig. 1f). The relative importance of turnover increases monotonically with  $\theta$  and  $M$   
289 (Fig. 1d). In a special case of 2 mainland species, the ratio of expected turnover and  
290 expected nestedness equals  $\theta$  (Fig. 1d). The Sørensen family indices have similar  
291 quantitative behaviors as the Jaccard family indices (see Fig. S1 in Appendix).

292

### 293 **Asymmetric islands (different colonization and extinction rates for two islands)**

294 The expected Jaccard dissimilarity conditional on both islands having non-zero  
295 species richness converges to  $\frac{(1+z)\theta}{1+(1+z)\theta}$  as  $M$  increases. But the deviation from

296  $\frac{(1+z)\theta}{1+(1+z)\theta}$  also increases with islands asymmetry  $z$  (Fig. 2a, e, i). The turnover

297 component increases monotonically with  $\theta$  and  $M$ , and decreases with  $z$  (Fig. 2b, f, j).

298 The nestedness component decreases with  $M$  when  $z$  is small (Fig. 2c), but this

299 relationship with  $M$  is reversed when  $z$  gets larger (Fig. 2g, k). The ratio of expected

300 turnover and expected nestedness also increases with  $M$  when  $z$  is small (Fig. 2d), and

301 decreases with  $M$  when  $z$  is large (Fig. 2h, l).

302

### 303 **Empirical test**

304 We tested the above predictions for an inland lake island system using 93 bird species

305 and 42 islands. We used an incidence function approach to fit the observed occupancy

306 patterns and calculated predicted alpha and beta diversity patterns from the fitted  
307 models. The non-neutral GLM has the lowest AIC and highest AUC in all models  
308 (Table 1). Among three neutral models, the neutral GLM model has the lowest AIC  
309 and the highest AUC. All models are better at predicting alpha diversity patterns than  
310 at predicting beta diversity patterns (Fig. 3). The neutral exponential model and GLM  
311 systematically underestimate the nestedness component, but overestimate the turnover  
312 component (Fig. 3f, j). In contrast, the neutral inverse ratio model systematically  
313 underestimates all observed pairwise beta diversity at the lower range of the  
314 predictions, yet it overestimates pairwise beta diversity at the higher range of the  
315 predictions (Fig. 3a-d). Both the neutral GLM and the non-neutral GLM successfully  
316 predict the observed alpha diversity pattern (Fig. 3i, m), but only the non-neutral  
317 GLM successfully predicts the observed beta diversity patterns (Fig. 3n-p).

318

319

## 320 **DISCUSSION**

### 321 **Theoretical results**

322 We derived a set of novel predictions of beta diversity patterns from the island  
323 biogeography theory. Under the classic MacArthur and Wilson framework, pairwise  
324 beta diversity patterns are determined by three factors: the size of the mainland  
325 species pool, extinction rates and colonization rates. Conditional on at least one island  
326 having species ( $N > 0$ ), only the expected Jaccard dissimilarity is independent of the  
327 size of mainland species pool. When conditioning on both islands having non-zero



328 richness ( $i+k > 0$  and  $j+k > 0$ ), all indices are dependent on the size of mainland  
329 species pool. Ignoring empty islands has a huge influence on beta diversity patterns  
330 when the size of mainland species pool is small (e.g. less than 10 species), but the  
331 effect becomes negligible toward larger mainland species pool sizes, because of the  
332 rapidly decreasing probability of empty islands (Fig. 1a). This result stresses the need  
333 to include empty islands in empirical tests of the island biogeography theory (Wang et  
334 al. 2016).

335

336 Pairwise Jaccard dissimilarity increases with relative extinction rates (the ratio  
337 between extinction rates and colonization rates). This is because when extinction  
338 events become more frequent the chance of forming “checkerboard” patterns  
339 (Diamond 1975) grows, as shown by the increasing turnover component (Fig. 1b).  
340 The nestedness component first increases then decreases with relative extinction rates  
341 (Fig. 1c). The maximum nestedness is achieved when extinction rates are less than  
342 colonization rates (Fig. 1c). When relative extinction rates or the size of mainland  
343 species pool gets larger, the increase of Jaccard dissimilarity is mainly driven by the  
344 increasing turnover component (Fig. 1d). Indices in Podani’s family (the replacement  
345 and richness difference components) have similar qualitative behaviors, consistent  
346 with previous finding that the partitioned components in Baselga’s family are  
347 correlated with the partitioned components in Podani’s family (Legendre 2014;  
348 Baselga and Leprieur 2015). Island asymmetry, which takes into account the effect of

349 isolation and area, does not change the qualitative behaviors of the indices (Fig 2), but  
350 increases the level of nestedness, because species in a small (distant) island are more  
351 likely to be a subset of species in a large (near) island.

352

### 353 **Neutral theory and null models**

354 Our theoretical results are derived from a species-level neutral theory. We show that  
355 both the neutral GLM and the non-neutral GLM are successful in predicting species  
356 richness (alpha diversity) of birds in the Thousand Islands Lake (Fig. 3i, m). But only  
357 the non-neutral model predicts the observed beta diversity patterns. The patterns of  
358 partitioned components further reveal that the neutral GLM fails to predict the  
359 observed pairwise Jaccard dissimilarity because it overestimates turnover and  
360 underestimates nestedness (Fig. 3j-l). Our analysis does not include biological factors  
361 that may cause species-level non-neutrality, but the presented framework is flexible to  
362 include such information if available.

363 Null models have become one of the most important tools in ecology. Despite their  
364 increasing popularity, it has also been recognized that their assumptions (e.g. the  
365 widely used random shuffling approaches) can have serious limitations, especially in  
366 the presence of multiple processes (Gotelli and Ulrich 2012; Pigot and Etienne 2015;  
367 Miller et al. 2017; O'Dwyer et al. 2017). In terms of beta diversity, the entangled  
368 links among alpha, beta and gamma diversity are known to reduce the statistical  
369 power of randomization tests and generate ambiguity in their interpretations (Chase et

370 al. 2011; Kraft et al. 2011; Qian et al. 2012, 2013; Ulrich et al. 2017). Our results  
371 support the use of mechanistic null models such as those based on neutral theory  
372 (O'Dwyer et al. 2009; Rosindell et al. 2012), maximum entropy theory (Xiao et al.  
373 2015, 2016; O'Dwyer et al. 2017), and incidence functions (Hanski et al. 1996; Helm  
374 et al. 2006; Hanski 2009) to improve upon random-shuffling null models in  
375 hypothesis testing. These mechanistic models could generate multiple diagnostic  
376 patterns and allows stronger test for ecological theories.

377

### 378 **Future directions**

379 Our results are derived from a mainland-island model where the colonization and  
380 extinction events on islands are independent of one another. More realistic  
381 modifications should be considered in order to predict biodiversity changes in a real  
382 landscape (Hanski 2009). For example, environmental heterogeneity and local  
383 dispersal are found to be important drivers of beta diversity in experimental studies  
384 (Grainger and Gilbert 2016; Gianuca et al. 2017; Ojima and Jiang 2017; Rodrigues  
385 and Diniz-Filho 2017). Moreover, in oceanic islands, high endemism arises from  
386 speciation events (Chen and He 2009; Gascuel et al. 2016; Steinbauer et al. 2016),  
387 which are likely to increase the level of species turnover. Future studies should also  
388 extend presence-based measures to abundance-based beta diversity measures which  
389 may provide additional insights into the dynamics of meta-community (Bashan et al.  
390 2016; Kalyuzhny and Shnerb 2017). We believe that the integration of beta diversity

391 patterns into the Theory of Island Biogeography offers new opportunities to infer  
392 community assembly processes.

393

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#### 397 **AUTHORSHIP**

398 ML and DV conceived of the idea. The idea was further developed with DV and WJ's  
399 input. ML conducted the analyses and wrote the manuscript. All authors assisted with  
400 revisions.

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- 632

633 Table 1. Models fitted to the presence-absence patterns of 93 bird species in 42  
 634 islands in the Thousand Island Lake, China.

Model	$\Delta$ AIC	AUC	Number of parameters	$R^2$		
				Richness	Dissimilarity	Turno
non-neutral.GLM	-2627	0.95	97	0.91	0.37	0.53
neutral.GLM	-172	0.61	5	0.90	0.01	0.45
neutral.exponential	-8	0.57	2	0.41	0.01	0.17
neutral.inverse ratio	1587	0.60	1	0.69	0.04	0.46
Total observation = 3906						

635 Note: For the neutral exponential model:  $c = \exp(-aI)$  and  $e = \exp(-bA)$ . For the  
 636 neutral inverse ratio model:  $c = \frac{a}{I}$  and  $e = \frac{b}{A}$ . Dissimilarity is the sum of turnover  
 637 component and nestedness component.  $\Delta$ AIC are calculated by subtracting the AIC of  
 638 the null model (GLM with only one intercept) from the AIC of the fitted model. AUC  
 639 are calculated with a Mann-Whitney U statistic.



640 **Figure legends**

641 Figure 1. Expected pairwise beta diversity of two identical islands (same colonization  
642 and extinction rates), conditioning on both islands having species ( $i > 0, j > 0$ ).  
643 Results are derived from the joint presence-absence distribution of two islands and  
644 shown for different mainland pool sizes. Blue dashed line in panel (a) is the analytical  
645 solution  $E(\text{Jaccard.dissimilarity}) = \frac{2\theta}{1+2\theta}$  for the case of at least one island having  
646 species ( $N > 0$ ). Relative extinction rate is the ratio of extinction rate and colonization  
647 rate.

648

649 Figure 2. Expected pairwise Jaccard beta diversities of two islands differing in  
650 colonization and/or extinction rates, conditioning on both islands having species ( $i > 0,$   
651  $j > 0$ ). The blue dashed line in panel (a), (e) and (i) are the analytical solutions of

652  $E(\text{Jaccard.dissimilarity}) = \frac{(1+z)\theta}{1+(1+z)\theta}$ , conditional on at least one island having

653 nonzero species. Expectations are provided for different levels of  $z$ , i.e. the number of  
654 times relative extinction rate on the second island exceeds that on the first. The black  
655 dashed lines in panel (d), (h) and (l) represent a 1:1 ratio. Different lines in a graph  
656 represent different mainland pool sizes (for color legend see Fig. 1).

657

658 Figure 3. Empirical evaluation of the theoretically fitted alpha and beta diversity  
659 patterns for the Thousand Islands Lake bird dataset. (a) - (l) are predictions of three  
660 neutral models, (m) - (p) are predictions of a non-neutral model. Solid black lines

661 represent a 1:1 relationship and dashed red lines are fits of ordinary linear regressions,

662 Point densities from high to low are color-coded from red to blue.

Figure 1

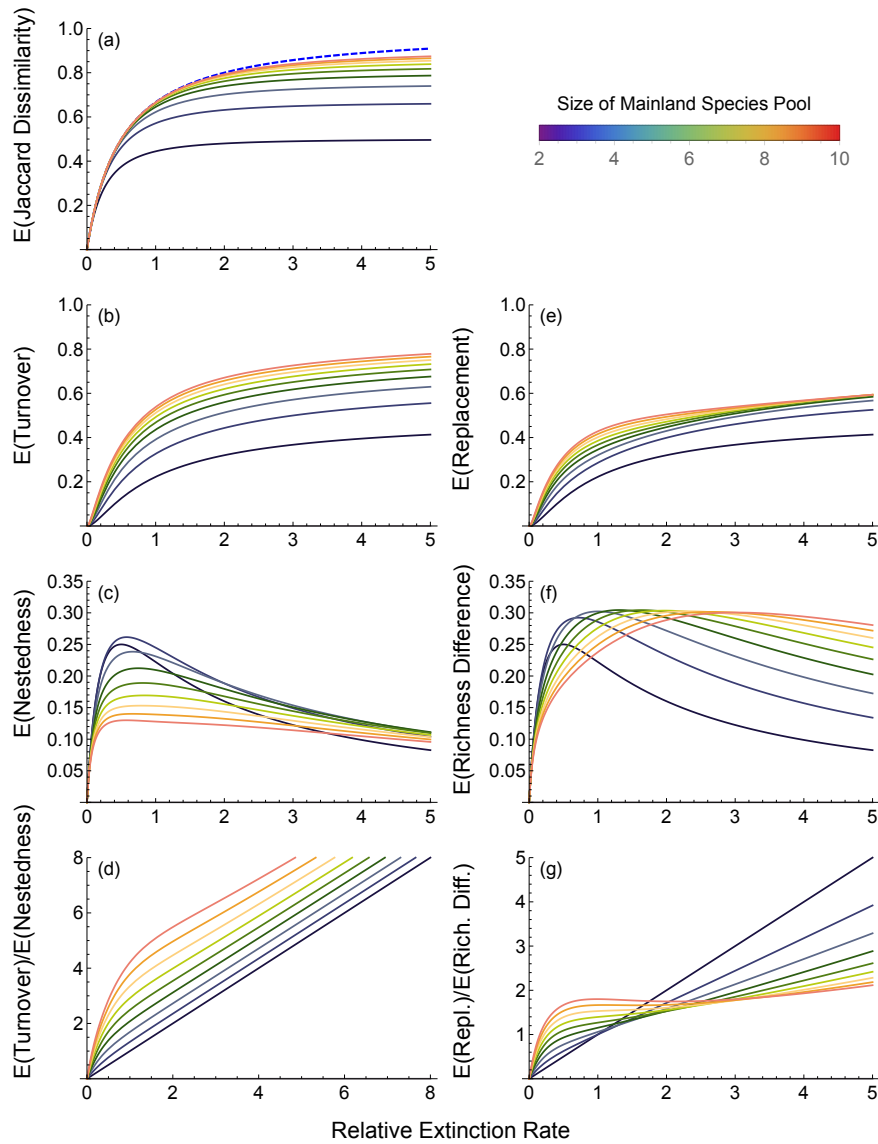


Figure 2

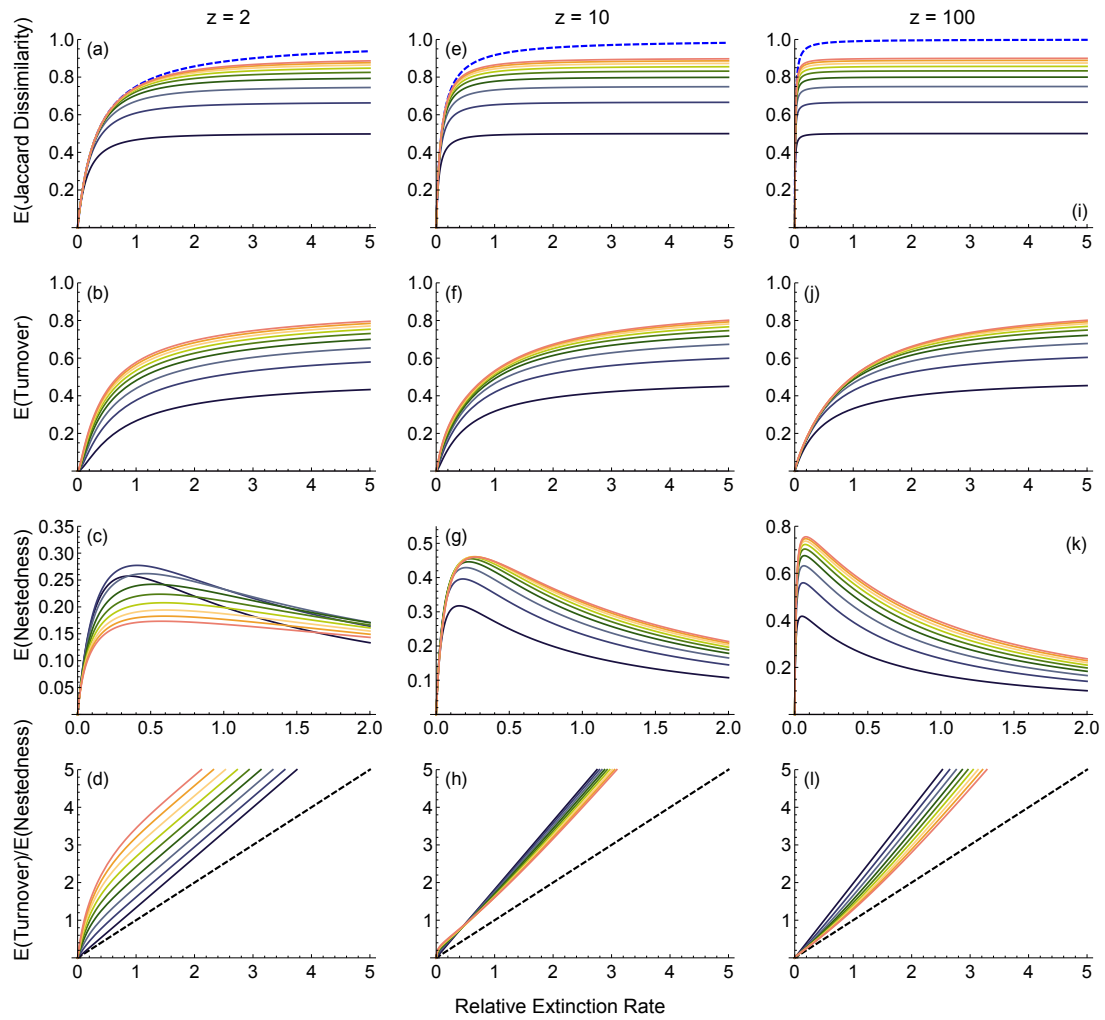


Figure 3

