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E-Article

Beta Diversity Patterns Derived from Island Biogeography Theory

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abstract: Metacommunity theory and its constituent theory of island biogeography (TIB) have the potential to unify ecology across different scales. The TIB has been successful in predicting alpha diversity patterns, such as species-area relationships and species-abundance distributions, but lags behind in predicting spatial beta diversity patterns. In this study we use island biogeography theory as the starting point to integrate spatial beta diversity patterns into metacommunity theory. We first derive theoretical predictions for the expected beta diversity patterns under the classic MacArthur and Wilson framework, where all species have equal colonization and extinction rates. We then test these predictions for the avian community composition of 42 islands (and 93 species) in Thousand Island Lake, China. Our theoretical results corroborate that longer distance and smaller area lead to higher beta diversity and further reveal that pairwise beta diversity is independent of the size of the mainland species pool. We also find that for the partitioned pairwise beta diversity components, the turnover component increases with the ratio of extinction rates and colonization rates, while the nestedness component is a unimodal function of the ratio of extinction rates and colonization rates. For the empirical island system, we find that beta diversity patterns better distinguish a species-equivalent model from a species-nonequivalent model than alpha diversity patterns. Our findings suggest that beta diversity patterns provide a powerful tool in detecting nonneutral processes, and our model has the potential to incorporate more biological realism in future analyses.

Keywords: neutral theory, null model, metacommunity, incidence function, community assembly, regional species pool.

Introduction

Metacommunity theory is at the frontier of unifying ecology across scales (Leibold et al. 2004; Leibold and Chase 2018), as it provides a natural way to integrate four fundamental processes in ecology—selection, drift, speciation, and dispersal (Vellend 2010). Integrating the theory of island biogeography (TIB), neutral theory, metapopulation theory, and metacommunity theory has been successful in explaining patterns such as species area relationships and species abundance distributions (Hensiques-Silva et al. 2013; Leibold and Chase 2018). But it has also become clear that our ability to infer processes is limited by the number of examined patterns. Increasing the dimensionality of the diagnostic patterns is thus crucial for further development of metacommunity theory (Leibold and Chase 2018).

One dimension of biodiversity that has been increasingly gaining attention in metacommunity studies is spatial beta diversity, which measures species compositional dissimilarity among communities. The concept of beta diversity was first introduced by Whittaker (1960, 1965) and was quickly linked to an array of important mechanisms in community assembly, such as biotic interactions (Graham and Fine 2008), environmental filtering (Veech and Crist 2007; Buckley and Jetz 2008), dispersal limitation (Ojima and Jiang 2017; Wu et al. 2017), and historical contingency (Fukami and Nakajima 2011). An important reason for the increasing prominence of beta diversity in metacommunity studies is the emergence of partitioning frameworks that have the potential to disentangle contributions of different processes, such as environmental filtering and competitive exclusions, to beta diversity patterns (Baselga 2010). Although the best way to partition pairwise beta diversity metrics remains debated (Baselga 2010; Podani and Schmera 2011; Legendre 2014; Baselga and Leprieur 2015), there is a general agreement that different measures quantify different aspects of communities and that their use should be guided by the research question (Anderson et al. 2011; Legendre 2014). Another value offered by beta diversity for metacommunity studies is its emergence as an effective tool to differentiate the niche model, where species have different resource or environmental requirements, and the neutral model, where all species are assumed to be the same (Chase and Myers 2011; Segre et al. 2014; Püttker et al. 2015). In a

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pure environmental niche model, beta diversity should be a function of distance in environmental space but independent of geographic distance; in contrast, in a pure neutral model, beta diversity should be a function of geographic distance but independent of environmental distance (Leibold and Chase 2018). Hubbell also showed that in a neutral model the distance decay of compositional similarity should be weaker in metacommunities with larger local community size or higher dispersal rates (2001). In reality, both niche process and neutral process contribute to observed beta diversity patterns (Legendre et al. 2005), together with additional factors such as species abundance distribution (Xu et al. 2015) and the size of the regional species pool (Chase et al. 2011; Kraft et al. 2011; Qian et al. 2013; Karger et al. 2015; Ulrich et al. 2017). Larger regional species pools are hypothesized to increase beta diversity because they allow more species to enter different local communities. Much progress has been made in measuring beta diversity (Chao et al. 2016), but analytical predictions from process-based theories remain rare and limited to abundance-based metrics, which calculate the probability of two random individuals belonging to the same species at a given distance (Chave and Leigh 2002; Condit et al. 2002; Zillio et al. 2005). A theoretical examination of beta diversity patterns based on an occupancy-based metacommunity model is still lacking.

We chose the TIB as the starting point for our work because it is the most parsimonious metacommunity model that has a constant species pool and because islands offer compelling study systems with growing global information (Weigelt et al. 2013; Patiño et al. 2017). The TIB (MacArthur and Wilson 1967) is most celebrated for elegantly linking species richness with colonization and extinction rates, which in turn are influenced by island area and distance to the mainland. Equilibrium TIB makes two key predictions: (1) equilibrium species richness depends on colonization and extinction rates and (2) the community composition of an island is undergoing constant turnover. While early empirical studies have focused on testing the equilibrium and temporal turnover predictions (Diamond 1969; Simberloff 1969; Simberloff and Wilson 1969, 1970; Diamond and May 1977), recent interest in the TIB lies in more complex processes, including allometric scaling (Jacquet et al. 2017), trophic interactions (Gravel et al. 2011; Cazelles et al. 2016), speciation (Chen and He 2009; Rosindell and Phillimore 2011; Rosindell and Harmon 2013), habitat heterogeneity (Kadmon and Allouche 2007), and island ontogenies (Whittaker et al. 2008; Borregaard et al. 2016). However, examinations to date have focused on alpha diversity patterns, such as species richness (MacArthur and Wilson 1967), species-abundance relationships (Rosindell and Phillimore 2011; Rosindell and Harmon 2013; Kessler and Shnerb 2015), functional diversity (Jacquet et al. 2017), and endemism (Chen and He 2009). A theoretical examination of beta diversity in the TIB is still missing. It is unclear how processes such as colonization and extinction shapes beta diversity patterns in the TIB.

In this study, we address this shortcoming and provide a theoretical integration of beta diversity into the TIB. Specifically, we present the first theoretical derivations for the expected pairwise beta diversity patterns for Jaccard dissimilarity under the classic MacArthur and Wilson framework. This framework is based on a species-level occupancy model where all species have the same colonization and extinction rates. We first derived the probability mass function of pairwise beta diversity and its expected value in a general case where the equilibrium assumption is not required. We then examined our results under the classic MacArthur-Wilson equilibrium framework and extended our discussion to N-community (multisite) beta diversity measures. Last, we tested the derived predictions for a data set of 93 avian species occurring across 42 islands of the Thousand Island Lake region in China (Wang et al. 2010).

Material and Methods

To derive the expected beta diversity patterns, we need to consider the joint statistical distribution of the occupancy patterns of multiple islands. We focus on pairwise community comparisons because the average pairwise dissimilarity is shown to be the only unbiased and consistent estimator when applied to empirical data (Marion et al. 2017). We also calculated the expected value of the partitioned components of pairwise beta dissimilarity for both the Baselga and the Podani families (Baselga 2010; Podani and Schmera 2011). To test our predictions, we applied the "incidence function" approach pioneered by Diamond (1975) and used by Connor and Simberloff (1978, 1979) during early debates of null models.

Probability Mass Function of Pairwise Beta Diversity

All pairwise beta diversity indices share the same probability mass function to describe island community composition because they are calculated from four quantities: the total number of species of two islands γ (regional species richness), the number of species shared by both islands k, the number of species unique to the first island i, and the number of species unique to the second island j (thus, $\gamma = k + i + j$).

Then the number of species present on the first island is $i + k$, and the number of species present on the second island is $j + k$. Denoting the size of the mainland species pool as M, the probability mass function of pairwise beta diversity, conditioning on γ, k, and i, can be derived as follows. Letting the occurrence probability of a species on the first island be p and a species on the second island be q, and furthermore assuming that the occurrence probabilities depend only on properties of islands rather than of species, the probability of obtaining exactly i unique species and k shared species from a species pool of size M on the first island is $p^{k+i}(1-p)^{M-(k+i)}$. Similarly, the probability of obtaining j unique and k shared species on the second island is $q^{k+j}(1-q)^{M-(k+j)}$, which yields the probability of obtaining the regional community specified by i, j, k, and M as the product $p^{k+i}(1-p)^{M-(k+i)}q^{k+j}(1-q)^{M-(k+j)}$.

We then count how many different combinations of island communities could be obtained with regional richness γ, k shared species, and i unique species to the first island (the number of unique species to the second island is then fixed as $k-i$). There are exactly $\mathrm{C}(M, \gamma)$ ways of choosing γ out of M species to be present in either or in both islands from the mainland species pool. Similarly, there are $\mathrm{C}(\gamma, k)$ ways to choose k out of γ species to be shared by both islands, and for the unique $\gamma-k$ species there are $\mathrm{C}(\gamma-k, i)$ ways of assigning i species to the first island. After simplification, the probability of pairwise beta diversity conditioning on the total number of species of both islands γ, the number of species shared by both islands k, and the number of species unique to the first island i is

$$\Pr(\text{regional.community}|\gamma, k, i) = \begin{bmatrix} M \\ \gamma \end{bmatrix}\begin{bmatrix} \gamma \\ k, i \end{bmatrix} p^{k+i}q^{k+j}(1-p)^{M-(k+i)}(1-q)^{M-(k+j)}. \tag{1}$$

Because beta diversity measures (e.g., Jaccard and Sørensen indices) are usually undefined at $\gamma = 0$, the expected pairwise beta diversity should be normalized by the term $1-(1-p)^M(1-q)^M$ to exclude "double-absence" scenarios (Anderson et al. 2011). Only the expected Jaccard dissimilarity

$$1 - \frac{k}{\gamma}$$

has a simple analytical form that is independent of the size of the mainland species pool M (for the derivation, see the appendix, available online; we do not show the analytical form of the expected Sørensen dissimilarity because the specific form depends on the size of the mainland species pool):

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

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

We also calculated the expected pairwise beta diversity for Jaccard and Sørensen families as well as their partitioned components (for detailed formulas of the Baselga and Podani families, see Baselga and Leprieur 2015) conditioning on both islands having species ($i+k>0$ and $j+k>0$) because empty islands are sometimes excluded from analysis (Wang et al. 2016). In Baselga's (2010) framework, the partitioned components are, respectively, the turnover component (which is different from the turnover metric used in Diamond and May 1977) and the nestedness component (different from the concept of nestedness in multisite measurements; Matthews et al. 2015). In Podani's (2011) framework the partitioned components are, respectively, the replacement component and the richness difference component. The turnover component in Baselga's framework and the replacement component in Podani's framework have the same numerator and account for species replacement in slightly different ways (Legendre 2014). The nestedness component in Baselga's framework only accounts for dissimilarity caused by richness differences derived from nested patterns, while the richness difference component in Podani's framework accounts for all kinds of richness differences (Baselga and Leprieur 2015). Although the Baselga's partitioned components and the Podani's partitioned components are related, they quantify different aspects of dissimilarity.

Island Biogeography Theory

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

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

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

$$p_{i,\mathrm{eq}} = \frac{c}{c+e}. \tag{4}$$

Let $\theta = e/c$, which is the relative extinction rate; equation (4) then becomes

$$p_{i,\mathrm{eq}} = \frac{1}{1+\theta}. \tag{5}$$

Substituting

$$p = q = \frac{1}{1+\theta}$$

into equation (2), the expected Jaccard dissimilarity when two islands have equal relative extinction rates is

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

To take into account asymmetry between islands (e.g., the effect of area, isolation, or habitat types), let

$$p = \frac{1}{1 + \theta}$$

and

$$q = \frac{1}{1 + z\theta},$$

so that the relative extinction rate on the second island is z times the relative extinction rate on the first island. Equation (2) becomes

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

We also simulated the scenario when two islands are identical but species have different relative extinction rates to assess the effect of interspecific variation as well as the effect of the shape of occurrence probability distribution (appendix).

N-Community Jaccard Dissimilarity

We further provide a heuristic link between pairwise Jaccard dissimilarity to N-community Jaccard dissimilarity in the TIB with a recent Hill's number framework (Chao et al. 2016). A class of regional (Jaccard-type) species-overlap measure is

$$U_{qN} = \frac{(1/{}^{q}D_{\beta})^{1-q} - (1/N)^{1-q}}{1 - (1/N)^{1-q}}, \tag{8}$$

where

$${}^{q}D_{\beta} = \frac{{}^{q}D_{\gamma}}{{}^{q}D_{\alpha}}. \tag{9}$$

The term q is the order of Hill's number, which in the case of presence-absence measure equals 0, and N is the number of total communities (islands). The terms ${}^{q}D_{\gamma}$, ${}^{q}D_{\alpha}$, and ${}^{q}D_{\beta}$ are, respectively, the effective regional diversity, the effective alpha diversity, and the effective beta diversity, the former two of which are just regional richness and local richness in the case of the presence-absence metric.

Under the TIB framework, expected regional richness (gamma diversity) is the size of the mainland species pool multiplied by the probability of having at least one species on one of the islands:

$${}^{q=0}D_{\gamma} = M\left[1 - \prod_{i}^{N}(1 - p_i)\right], \tag{10}$$

where p_i is the occurrence probability of a species on island i.

The expected alpha diversity is the size of the mainland species pool multiplied by the sum of occurrence probabilities of all of the islands:

$${}^{q=0}D_{a} = M\sum_{i}^{N} p_i. \tag{11}$$

Combining equations (8)–(11) and setting

$$N = 2,$$
$$p_1 = p,$$
$$p_2 = q,$$

which corresponds to the pairwise situation, we get the pairwise Jaccard similarity

$$U_{q=0,N=2} = \frac{pq}{p + q - pq}, \tag{12}$$

which is the same with what we derived in equation (2) once we subtract (12) from 1. But this does not mean that we could automatically get the expected N-community Jaccard dissimilarity for $N > 2$ unless

$$E(D_{\beta}) = E(D_{\gamma})/E(D_{\alpha})$$

is always true. However, in the special case where N approaches infinity and

$$E(D_{\gamma}) = M,$$

we could use (5) and (8)–(11) to derive the expected N-communities Jaccard similarity, which is just the ratio between alpha diversity and gamma diversity assuming that all islands are the same:

$$U_{q=0,N\to\infty} = \frac{{}^{q=0}D_{\alpha}}{{}^{q=0}D_{\gamma}} = p_{i,\text{eq}} = \frac{1}{1 + \theta}. \tag{13}$$

Empirical Tests

Data. We used a published data set of avian community composition for 93 birds and 42 islands in Thousand Island Lake, China, to test our predictions (see the appendix in Wang et al. 2010). The region (29°22″–29°50″N, 118°34″–119°15″E) consists of an inundated lake with more than 1,000 islands created by dam constructions in 1959. Because the islands were formed recently, it is unlikely that there has been in situ speciation in this region. The relatively small area of the region (573 km^2) ensures that the islands are accessible to most of the bird species (Si et al. 2016). Bird occupancies from 2006 to 2009 on 42 islands were documented using the line-transect method. Island variables measured in the data set include area, distance to mainland, habitat diversity (the number of habitat types within an island), and vascular plant species richness (table 1).

Table 1: Summary statistics for islands in Thousand Island Lake, China

Island	Area (ha)	Isolation (m)	No. habitat types	Plant richness
1	1,289.23	897.41	7	198
2	143.19	1,415.09	6	99
3	109.03	964.97	6	86
4	55.08	953.95	5	59
5	46.37	729.8	5	51
6	35.64	2,110.41	5	49
7	32.29	1,936.95	5	57
10	5.69	21.85	3	69
11	3.42	583	4	74
12	2.9	1,785.3	3	85
13	2.83	1,238.14	4	86
14	2.29	973.85	4	65
15	2.23	3,261.96	3	53
16	2	1,042.38	3	45
17	1.93	888.05	4	50
18	1.74	2,293.25	3	100
20	1.54	711.04	3	88
21	1.52	849.88	3	40
22	1.52	2,849.99	3	53
23	1.4	1,760.34	3	49
24	1.26	54.86	3	65
25	1.2	657.72	3	56
26	1.2	2,128.52	3	68
27	1.17	2,453.37	3	69
28	1.15	847.12	3	33
30	1.03	1,458.81	3	36
31	1.01	2,437.85	3	29
32	1.01	2,103.85	3	36
33	.97	938.85	3	70
34	.96	3,133.96	3	50
35	.91	1,339.71	4	50
36	.86	2,321.51	3	56
37	.83	2,298.5	3	50
38	.83	1,098.58	4	45
39	.8	102.6	3	68
40	.8	2,097.52	2	80
41	.73	1,320.4	3	31
42	.67	1,139.87	3	39
43	.59	640.53	3	42
44	.59	1,018.42	3	55
45	.57	3,712.31	3	47
46	.3	1,086.03	2	75

Note: Plant richness refers only to vascular plant richness. The original table of island variables can be found in Wang et al. (2010).

Incidence Function and Statistical Analysis. Because extinction rates and colonization rates are difficult to measure directly, an alternative way is to use an incidence function approach to estimate parameters from a snapshot of occupancy patterns (Diamond 1975; Hanski 2009). To test the predictions of island biogeography theory, equation (4) is modeled as a function of isolation and area. We first constructed our own binomial likelihood function with different assumptions for the relationship between extinction rates and area and the relationship between colonization rates and isolation. Then we used the nlm function in the R package stat to fit the maximum likelihood parameters for the first two models. We expected that the species-equivalent generalized linear model (GLM) would have an overall better performance than any other model based solely on isolation and area information because it allows for the incorporation of other variables. Therefore, we chose only two species-equivalent models to capture different colonization-isolation and extinction-area relationships mostly for their mathematical tractability and easier convergence in fitting.

Species-equivalent model 1: inverse ratio. Colonization rates are modeled as an inverse ratio function of isolation (I),

$$c = \frac{a}{I},$$

and extinction rates are modeled as an inverse ratio of area (A),

$$e = \frac{b}{A},$$

where a and b are parameters. In actual fitting, a and b are reduced to one parameter.

Species-equivalent model 2: exponential. Colonization rates are modeled as an exponential function of isolation,

$$c = \exp(-aI),$$

and extinction rates are modeled as an exponential function of area,

$$e = \exp(-bA),$$

where a and b are fitted parameters. Substitute

$$c = \exp(-aI)$$

and

$$e = \exp(-bA)$$

into equation (4), and the occurrence probability becomes

$$p = \frac{1}{1 + \exp(-bA + aI)}.$$

Thus, the exponential species-equivalent model is equivalent to a logistic regression without intercept, which could be directly fitted by the glm function in the R package stats with a binomial distribution and logit link.

Species-equivalent model 3: GLM. This model adds habitat diversity and vascular plant richness to the predictors in addition to area and isolation in species-equivalent model 2. The Akaike information criterion (AIC) is used to select the best model (Burnham and Anderson 2004). Area and isolation are log transformed for better linearity.

Species-nonequivalent model: aggregate species-level GLM. To take into account interspecific variation in occurrence probabilities, species identity is included as a fixed effect categorical variable in the GLM, which allows each species to have a different intercept (baseline occurrence probability) but share the same response to island area, isolation, plant richness, and habitat types. This is essentially a stacked species distribution modeling approach (Calabrese et al. 2014; Ko et al. 2016), which increases the number of parameters by the number of species minus one (92 parameters in this case). This procedure aims to capture the observed presence-absence variation among species but does not pin down the causes of interspecific variation, such as traits and differences in abundance. More realistic assumptions of species nonequivalence, such as different responses to area and isolation, could be made but are not the main focus of this paper. Area under the curve (AUC) and AIC values are calculated to compare the overall performance of the models. AUC is calculated with a Mann-Whitney U statistic using the R package PresenceAbsence (Freeman and Moisen 2008). AIC is calculated from the best-fit likelihood function (Burnham and Anderson 2004). ΔAIC is calculated by subtracting the AIC of the null model (GLM with only the intercept) from the AIC of the fitted model.

Predictions of Alpha Diversity and Beta Diversity

The predicted species richness of each island is given by the summed fitted occurrence probabilities of all species, as used in conventional stacked species distribution modeling (Calabrese et al. 2014; Ko et al. 2016). While predicted pairwise Jaccard dissimilarity can be calculated analytically from equation (2), the partitioned nestedness and turnover components can be estimated only by simulations.

For the clarity of demonstrating the strength of a partitioned framework, we present only the results of Baselga's family, although Podani's family could be similarly calculated. We therefore estimate predicted pairwise beta diversity as the mean of 1,000 community matrices simulated from the fitted occurrence probabilities. Observed values are regressed against predicted values using ordinary least squares. R^2 is used as a measure of predictive power for alpha and beta diversity patterns. If the model predicts the observed patterns well, then the fitted regression line should be close to the 1∶1 ratio line when observed values are plotted against predicted values. All statistical analyses are performed in R version 3.3.2. Code is provided in a zip file, available online.[1]

Results

Symmetric Islands (Same Colonization and Extinction Rates for Both Islands)

The expected Jaccard dissimilarity conditioned on both islands having nonzero species richness increases with relative extinction rate θ and the size (number of species) of the mainland species pool M. As M increases, the expected Jaccard dissimilarity converges to

$$\frac{2\theta}{1+2\theta}$$

(fig. 1*a*). When decomposed into turnover and nestedness (or replacement and richness difference) components, contrasting patterns are observed: while the turnover component and the replacement component increase monotonically with θ and M (fig. 1*b*, 1*e*), the nestedness component and the richness difference component are both unimodal functions of θ with maximum values less than 0.3 (fig. 1*c*, 1*f*). The maximum nestedness decreases as M increases (fig. 1*c*), while the maximum richness difference changes less with the increase of M (fig. 1*f*). The ratio of expected turnover to expected nestedness increases with θ and M (fig. 1*d*). In the special case of two mainland species, the ratio of expected turnover and expected nestedness equals θ (fig. 1*d*). The Sørensen family indices have qualitatively similar but quantitatively nonequivalent behaviors compared with the Jaccard family indices (see fig. A1; figs. A1–A4 are available online). Introducing interspecific variation in relative extinction rates reduces the total amount of beta diversity as well as the turnover component (fig. A2). For $M > 50$, the effect of the size of the mainland species pool on mean beta diversity is negligible. Increasing the size of the mainland species pool only decreases the variance of beta diversity (fig. A2). Increasing unevenness of the occurrence probability leads to lower beta diversity (figs. A3, A4)

Asymmetric Islands (Different Colonization and Extinction Rates for Two Islands)

The expected Jaccard dissimilarity conditioned on both islands having nonzero species richness converges to

$$\frac{(1+z)\theta}{1+(1+z)\theta}$$

as M increases. But the deviation from

$$\frac{(1+z)\theta}{1+(1+z)\theta}$$

also increases with island asymmetry z (fig. 2*a*, 2*e*, 2*i*). The turnover component increases monotonically with θ and M and decreases with z (fig. 2*b*, 2*f*, 2*j*). The nestedness component

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[1] Code that appears in *The American Naturalist* is provided as a convenience to readers. It has not necessarily been tested as part of peer review.

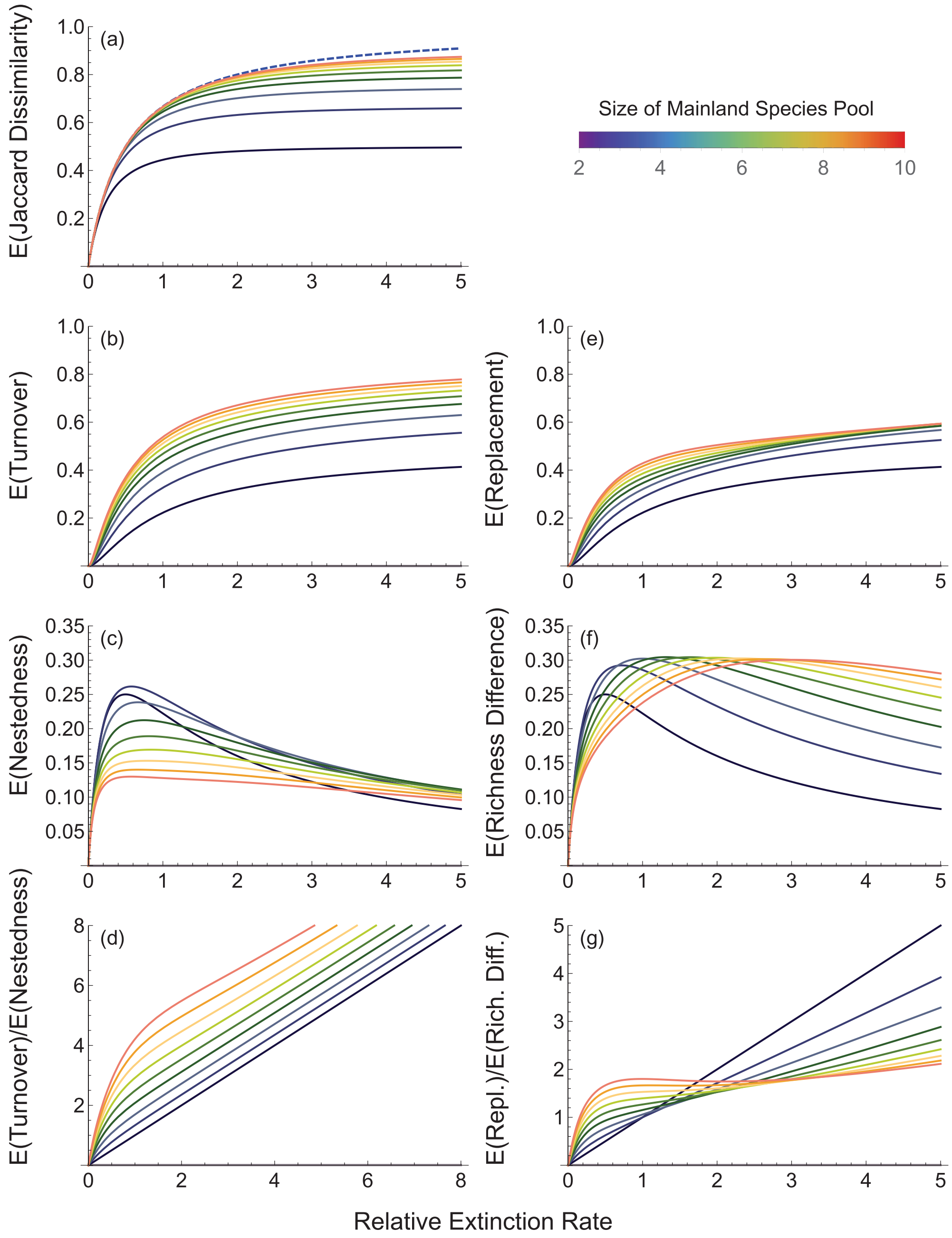

Figure 1: Expected pairwise Jaccard beta diversities (*Y*-axes) of two identical islands (same colonization and extinction rates), conditioned on both islands having species. Results are derived from the joint presence-absence distribution of two islands and shown for different mainland pool sizes. The blue dashed line in *a* is the analytical solution $\mathrm{E(Jaccard.dissimilarity)} = 2\theta/(1 + 2\theta)$ for the case of at least one island having species. The relative extinction rate is the ratio of the extinction rate and the colonization rate.

decreases with M when z is small (fig. 2*c*), but this relationship with M is reversed when z gets larger (fig. 2*g*, 2*k*). There is also less variability with M for the nestedness component as z increases. The ratio of expected turnover and expected nestedness also increases with M when z is small (fig. 2*d*) and decreases with M when z is large (fig. 2*h*, 2*l*).

Empirical Test

We tested some of the predictions described above for an inland lake island system using 93 bird species and 42 islands. We used an incidence function approach to fit the observed occupancy patterns and calculated predicted alpha

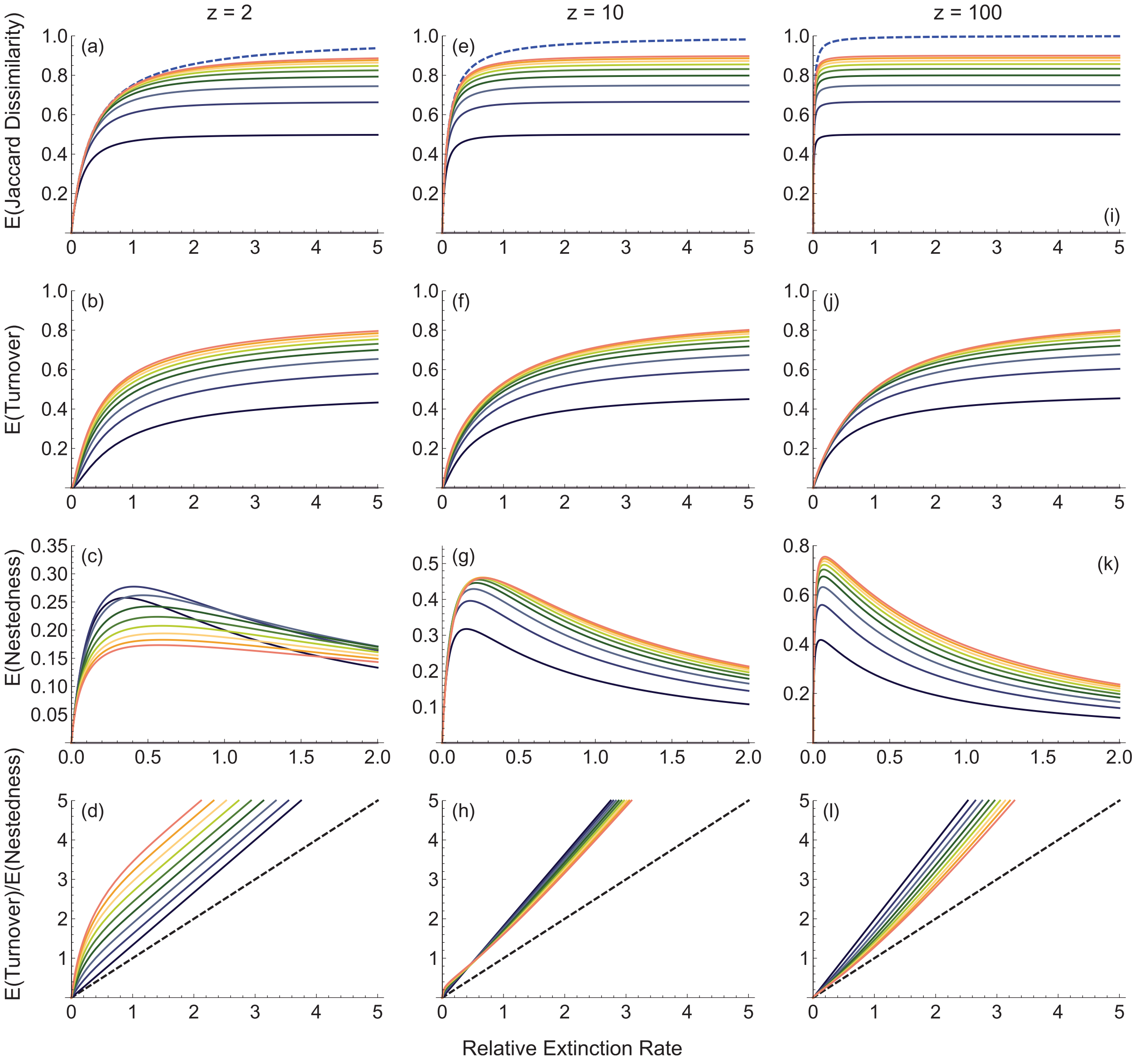

Figure 2: Expected pairwise Jaccard beta diversities of two islands (Y-axes) differing in colonization and/or extinction rates, conditioned on both islands having species. The blue dashed lines in *a*, *e*, and *i* are the analytical solutions of $\mathrm{E(Jaccard.dissimilarity)} = ([1 + z]\theta)/(1 + [1 + z]\theta)$, conditioned on at least one island having nonzero species. Expectations are provided for different levels of z, that is, the number of times the relative extinction rate on the second island exceeds that on the first. The black dashed lines in *d*, *h*, and *l* represent a 1:1 ratio. Different lines in a graph represent different mainland pool sizes (for color key, see fig. 1).

and beta diversity patterns from the fitted models. The species-nonequivalent GLM has the lowest AIC and the highest AUC of all models (table 2). Among three species-equivalent models, the GLM has the lowest AIC and the highest AUC. All models are better at predicting alpha diversity patterns than at predicting beta diversity patterns (fig. 3). The species-equivalent exponential model and GLM systematically underestimate the nestedness component but overestimate the turnover component (fig. 3*f*–3*h*, 3*j*–3*l*). In contrast, the species-equivalent inverse ratio model systematically underestimates all observed pairwise beta diversity at the lower range of the predictions, yet it overestimates pairwise beta diversity at the higher range of the predictions (fig. 3*a*–3*d*). Both the species-equivalent GLM and the species-nonequivalent GLM successfully predict the observed alpha diversity pattern (fig. 3*i*, 3*m*), but only the species-nonequivalent

Table 2: Models fitted to the presence-absence patterns of 93 bird species in 42 islands in Thousand Island Lake, China

				R^2			
	Estimate	ΔAIC	AUC	Richness	Dissimilarity	Turnover	Nestedness
Species nonequivalent GLM	log(Isolation): $-.22^{***}$ log(Area): $.54^{***}$ Plant richness: $.0065^{**}$	−2,627	.949	.91	.37	.53	.75
Species equivalent GLM	log(Isolation): $-.079^{*}$ log(Area): $.21^{***}$ Plant richness: $.0038^{*}$	−172	.605	.9	.01	.45	.68
Species-equivalent exponential	a: $.0005^{***}$ b: $.0015^{***}$	−8	.569	.41	.01	.17	.26
Species-equivalent inverse ratio	d: $.0063^{***}$	1,587	.603	.69	.04	.46	.56

Note: For the species-equivalent exponential model, $c = \exp(-aI)$ and $e = \exp(-bA)$. For the species-equivalent inverse ratio model, $c = a/I$, $e = b/A$, and $d = b/a$. Dissimilarity is the sum of the turnover component and the nestedness component. Area under the curve (AUC) is calculated with a Mann-Whitney U statistic. AIC = Akaike information criterion.

[*] $P < .05$.

[**] $P < .01$.

[***] $P < .001$.

GLM successfully predicts the observed beta diversity patterns (fig. 3*n*–3*p*).

Discussion

Theoretical Results

We demonstrate the mechanistic link of beta diversity patterns to the extinction rates and colonization rates of species in islands, which has been lacking in previous developments of island biogeography theory (Santos et al. 2016; Patiño et al. 2017). Part of our theoretical results echo what the neutral theory predicts about the effect of distance (isolation) and local community size (which in the neutral theory is proportional to area): longer distance and lower dispersal rates increase beta diversity, while larger area reduces beta diversity (Hubbell 2001; Chave et al. 2002; Kraft et al. 2011). But other parts of our theoretical results reveal novel insights about the formation of beta diversity, such as the effect of regional species pool and behaviors of the partitioned pairwise beta diversity components.

There is a heated debate about the effect of gamma diversity or the richness of the regional species pool on beta diversity patterns (Kraft et al. 2011; Qian et al. 2012, 2013; Ulrich et al. 2017). The usual assumption is that a larger species pool should increase beta diversity because it allows more species to enter different communities. But our results show that in the classic island biogeography model the expected pairwise Jaccard dissimilarity is independent of the size of the mainland species pool. In other words, as long as all species in the regional pool have the same occurrence probability on an island, the species compositional difference of any two islands will be the same no matter how many species are there in the pool. The dependence of beta diversity on the size of the mainland species pool in figure 1 results from renormalizing the joint probability distribution of island occupancy by excluding the probability when one of the islands is empty. Our simulations further confirm that even in the presence of interspecific variation in occurrence probabilities, the size of the mainland species pool does not significantly change expected beta diversity (fig. A2). This implies that the species pool effect is more likely to act indirectly through other factors, such as species abundance distribution (Xu et al. 2015) or functional diversity (Patrick and Brown 2018) instead of richness per se. The frequency distribution of occurrence probabilities in the simulation also reveals that the deviation from species-equivalent expectation could be caused by species abundance distribution (fig. A3). As beta diversity is a measure of the proportion of shared species, any inequality in occurrence probabilities should increase the relative prevalence of more abundant species, thus decreasing overall beta diversity. This result is corroborated by our simulations (fig. A4). But we also caution against overinterpreting our results in relation to previous studies because prior work often used a different beta diversity metric (which might change the relationship between beta diversity and the size of species pool) and fixed local community sizes (as opposed to dynamic sizes in the TIB).

By partitioning pairwise Jaccard dissimilarity into the nestedness and the turnover components, we reveal how the proportions of these two independent components change with extinction and colonization rates. One key result is that the relative importance of the turnover component increases nearly linearly with higher extinction rates, which shows that

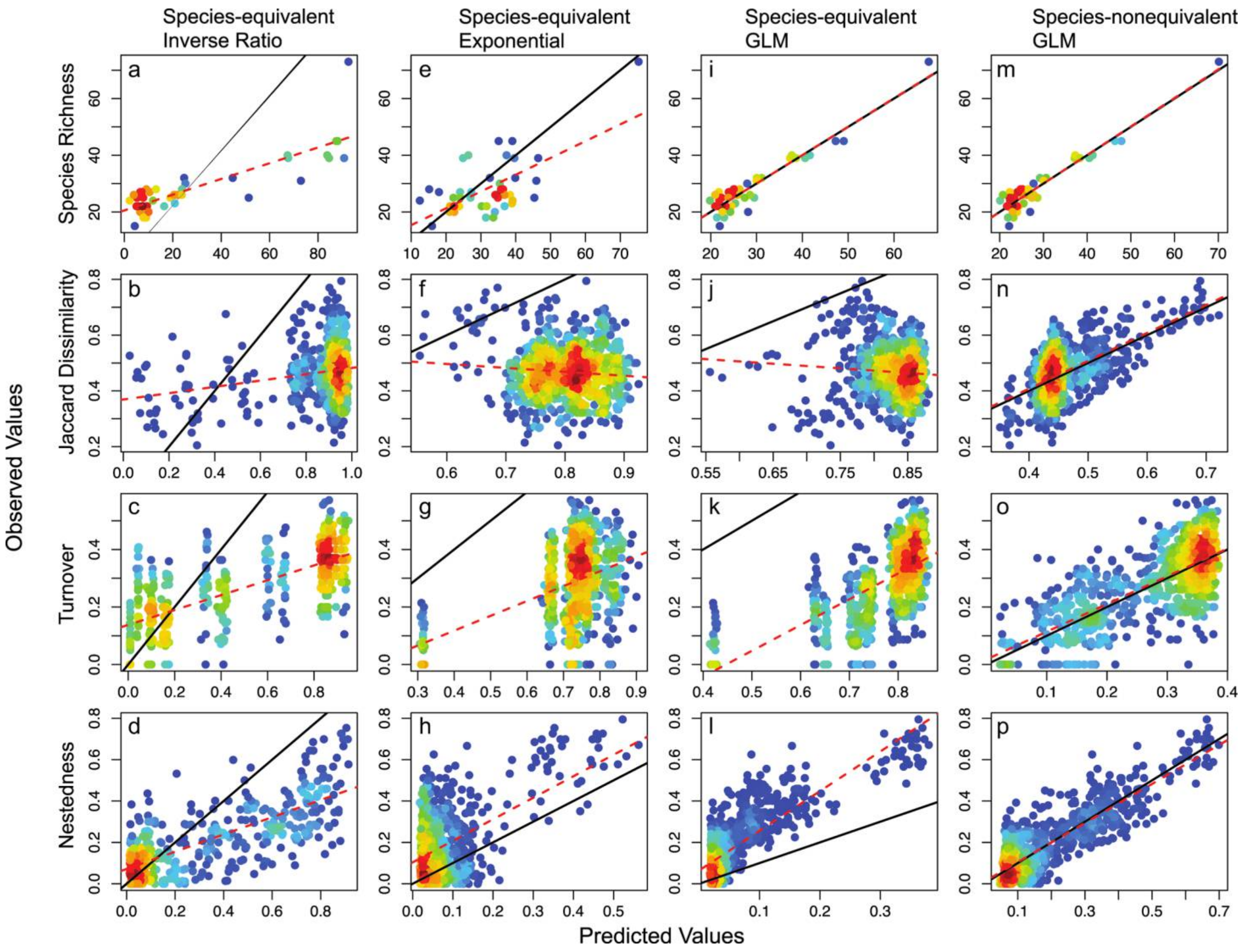

Figure 3: Empirical evaluation of the theoretically fitted alpha and beta diversity patterns for the Thousand Island Lake bird data set. *a–l* are predictions of three species-equivalent models, and *m–p* are predictions of a species-nonequivalent model. Solid black lines represent a 1:1 relationship, and dashed red lines are fits of ordinary linear regressions. Point densities from high to low are color coded from red to blue. GLM = generalized linear model.

the turnover component has great potential to reveal accelerated extinction events (Baselga and Leprieur 2015). A larger proportion of the nestedness component might reflect that processes other than ecological drift (such as historical contingency) have a greater contribution to community assembly (Leprieur et al. 2011). The relationships between Podani's partitioned components with relative extinction rates are similar but not equivalent to Baselga's partitioned components (fig. A2). This might have further implications for more complex metacommunity models, where a richness difference gradient metacommunity does not correspond to a nestedness gradient metacommunity. We did not fully explore these differences, and they remain an area worthy of future work.

Last, we provide the first theoretical prediction of an *N*-community beta diversity metric, which is increasingly gaining attention in recent literature because of the rich biodiversity information they supply (Hui and McGeoch 2014; Arita 2017; Latombe et al. 2017). Even though we cannot derive expected *N*-community Jaccard similarity for all *N* bigger than two and less than infinity, we can calculate the ratio between expected alpha diversity and expected gamma diversity from equations (10) and (11), which should approximate the expected Jaccard similarity at equilibrium (Chase et al. 2011). The ratio of equations (10) and (11) is

$$\frac{\sum_i^N p_i}{1-\prod_i^N(1-p_i)}.$$

It could be rewritten as

$$\frac{N\bar{p}}{1-[G(1-p)]^n},$$

where $\bar{p}$ and $G(1-p)$ are, respectively, the arithmetic mean of all p_i and the geometric mean of all $(1-p_i)$, which immediately shows that habitat heterogeneity (by drawing p_i from a statistical distribution) is always going to increase *N*-community beta diversity because the maximum value of $G(1-p)$ is reached when all p_is are equal.

Empirical Test

We tested the empirical beta diversity patterns of the Thousand Island Lake bird data set against various models as a proof of concept to demonstrate that occupancy-based models have much to offer in terms of linking theoretical predictions to empirical patterns. We show that both the species-equivalent GLM and the species-nonequivalent GLM are successful in predicting species richness (alpha diversity) of birds in Thousand Island Lake (fig. 3*i*, 3*m*). But only the species-nonequivalent model predicts the observed beta diversity patterns. We suggest that the lower sensitivity of the alpha diversity pattern to nonneutral processes is caused by the fact that species richness is ignorant of species identity and co-occurrence patterns and thus is less likely to detect nonrandom species-habitat associations. The patterns of partitioned components further reveal that the species-equivalent GLM fails to predict the observed pairwise Jaccard dissimilarity because it overestimates the turnover component and underestimates the nestedness component (fig. 3*j*–3*l*). A thorough investigation of why the empirical pattern deviates from the species-equivalent model is beyond the scope of this study, but a few factors are likely to contribute to the species-specific occupancy variation: (1) variation in abundance among the species translates into differences in occurrence probability, (2) differences in dispersal traits cause variation in colonization rates among islands, (3) species-specific habitat preferences intersect with habitat differences among islands, and (4) anthropogenic activities cause selective extinctions. Recent evidence suggests that all of these factors have contributed to shaping beta diversity patterns in Thousand Island Lake (Si et al. 2016; Wu et al. 2017; Liu et al. 2018). A more rigorous test of the TIB thus will involve estimating actual turnover and extinction rates using time-series data (Si et al. 2014).

Our method belongs to a group of mechanistic null models (O'Dwyer et al. 2017) that differ from random shuffling null models (Ulrich and Gotelli 2013) by explicitly incorporating process parameters such as extinction and colonization rates into the model. In terms of beta diversity, the entangled links among alpha, beta, and gamma diversity are known to reduce the statistical power of randomization tests and bring ambiguity to their interpretations (Chase et al. 2011; Kraft et al. 2011; Qian et al. 2012, 2013; Ulrich et al. 2017). Our results support the use of mechanistic null models such as those based on neutral theory (O'Dwyer et al. 2009; Rosindell et al. 2012), maximum entropy theory (Xiao et al. 2015, 2016; O'Dwyer et al. 2017), and incidence functions (Hanski et al. 1996; Helm et al. 2006; Hanski 2009) to improve on random-shuffling null models in hypothesis testing.

Conclusions and Future Directions

In this article, we studied the beta diversity patterns of a simple metacommunity model: the island biogeography model. But to understand more complex community assembly processes and to enhance the transferability of the theory to mainland applications, more biological realism should be considered in the future. For example, local dispersal is known to interact with disturbance (Ojima and Jiang 2017), environmental heterogeneity (Gianuca et al. 2017), and priority effects (Vannette and Fukami 2014, 2017) to create complex beta diversity patterns that deserve in-depth theoretical examinations. Local dispersal could be incorporated into our model by making the occurrence probability of an island dependent on immigrations from neighboring islands. Another important process that is missing in our model is speciation. Studying how speciation influences beta diversity patterns is crucial for understanding the origins and maintenance of biodiversity in oceanic islands (Cabral et al. 2014). We believe that the integration of beta diversity patterns into the TIB offers new opportunities for inferring community assembly processes and developing a unified metacommunity theory.

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