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Complex relationships between beta diversity and dispersal in meta-community models

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Dispersal is one of the most important drivers of community assembly. Understanding how dispersal impacts spatial variations in community composition (beta diversity) is crucial for predicting biodiversity change during the Anthropocene. Classic theories and a large amount of empirical evidence have led to a common belief that increasing dispersal rate should lead to regional community homogenization (lower beta diversity). However, recent empirical studies show that increasing dispersal can also lead to regional community divergence when interacting with other processes such as disturbance and priority effect. The underappreciation of the complex relationship between beta diversity and dispersal might impede our ability to make accurate ecological forecasts. To address this concern, I examine the beta diversity–dispersal relationship through extinction and colonization dynamics in meta-community models. I find that a wide range of beta diversity–dispersal relationships (e.g. negative, positive, hump-shaped) can be generated by changes in species-level occurrence probabilities when meta-population dispersal (rather than mainland–island dispersal), disturbance and strong biotic interactions are at play. Specifically, reducing the variance of species-level occurrence probabilities leads to community divergence and increasing the mean occurrence probability leads to community homogenization; a positive or hump-shaped beta diversity–dispersal relationship emerges when the effect of the decreasing variance is stronger than the effect of increasing mean. These findings highlight the intrinsic constraint of occupancy stochasticity on beta diversity changes and echo the call for more realistic manipulations of stochastic dispersal and a detailed understanding of the interaction networks to test various beta diversity–dispersal relationships in future empirical studies.

Keywords: biotic interactions, checkerboard distribution, island biogeography theory, local dispersal, meta-community, meta-population model, neutral theory, species co-occurrence

Introduction

Understanding the bewildering diversity and complexity of nature is a fundamental goal of ecology. Species co-occurrence or compositional variation among communities (i.e. beta diversity, high value indicates dissimilar communities) is at the heart of this pursuit. Why do some species always co-occur, and why are some communities

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so distinct? These questions have stimulated heated discussions about the mechanisms of community assembly: from Clements and Gleason's arguments over climax community (Clements 1916, Gleason 1926), Diamond and Simberloff's debates over checkerboard distributions (Connor and Simberloff 1978, 1979, Connor et al. 2015, Diamond et al. 2015), the rebuttals over the drivers of latitudinal beta diversity gradients (Kraft et al. 2011, Qian et al. 2013, Xu et al. 2015, Sreekar et al. 2018, Xing and He 2019), to the debates over the relative importance of neutral stochasticity and niche-based processes (Chase and Myers 2011, Mori et al. 2015, Rael et al. 2018, Ning et al. 2019). The discussions about beta diversity not only contributed to the development of statistical tools to inform biodiversity conservations (Ferrier et al. 2007, McKnight et al. 2007, Legendre 2014, Socolar et al. 2016) but also helped to uncover the link between microbiome composition and human health (Yatsunenko et al. 2012, Bashan et al. 2016, Rothschild et al. 2018).

Dispersal, one of the most fundamental processes in community assembly, has always been the focus of ecological studies. It not only inspired the classic island biogeography theory (MacArthur and Wilson 1967), meta-population theory (Levins 1969), neutral theory (Hubbell 2001) and meta-community theory (Leibold and Chase 2018) but also received more and more practical concerns over its impact on ecosystem stability (Howeth and Leibold 2010, Abbott 2011, Baron and Galla 2020) and functioning (France and Duffy 2006, Thompson et al. 2017, 2020).

Classic theories examine the relationship between dispersal and compositional variation (beta diversity) through the lens of local and regional species richness because the ratio between gamma diversity (regional richness) and alpha diversity (local richness) is a measure of beta diversity (Whittaker 1960): the island biogeography theory and the neutral theory predict that local communities become more similar in composition (homogenization) when dispersal increases because alpha diversity increases faster than gamma diversity (Hubbell 2001, Lu et al. 2019); previous metacommunity models also predict that dispersal leads to community homogenization as a consequence of competitive exclusions at the regional scale (decreasing gamma diversity) despite that alpha diversity peaks at the intermediate level of dispersal (Mouquet and Loreau 2003, Thompson et al. 2020).

Although various relationships between dispersal and alpha or gamma diversity (positive, negative and hump-shaped relationship) have been detected empirically (Cadotte 2006, Myers and Harms 2009, Grainger and Gilbert 2016), the negative beta diversity–dispersal relationship (dispersal leads to community homogenization) is remarkably consistent across studies (Grainger and Gilbert 2016, Catano et al. 2017). Because of the abundance of evidence in favor of the homogenization effect of dispersal, the other side of the story – that increasing dispersal rate could lead to community divergence – has been largely overlooked. This neglect may result in an underappreciation of the complexity of meta-community dynamics: Vannette and Fukami (2017) show that increasing dispersal among flowers can lead to microbial community divergence due to priority effects (i.e. different arrival history creates different stable states); Ojima and Jiang (2017) find that increasing dispersal resulted in community homogenization only in the absence of disturbance; in a meta-analysis on herbaceous plants, Catano and colleagues (2017) show that increasing dispersal led to community divergence in the presence of disturbance in 2 out of 22 studies.

In a word, the beta diversity–dispersal relationship is far from straightforward.

In general, all changes in community dissimilarity can be traced back to colonization and extinction events: increasing the number of widespread species by colonization or decreasing the number of range-restricted species by extinction will lead to community homogenization; while increasing the number of range-restricted species by colonization or decreasing the number of widespread species by extinction will lead to community divergence (Tatsumi et al. 2020, 2021). In light of species-level occurrence probabilities, increasing the mean occurrence probability of species (which is equivalent to increasing alpha diversity) will lead to community homogenization because of the increase of widespread species; while decreasing the variance of occurrence probabilities will lead to community divergence (Lu et al. 2019) because of the decrease of widespread species. From previous empirical work, I identified three potentially important drivers that give rise to the positive beta diversity–dispersal relationship: stochastic dispersal, disturbance and biotic interactions.

Stochastic dispersal creates variance in arrival histories and contributes to the increase of range-restricted species by colonization, therefore increasing the chance of community divergence (Fukami and Nakajima 2011, Pu and Jiang 2015, Vannette and Fukami 2017). There are two ways of incorporating dispersal stochasticity in ecological theories (Vellend et al. 2014): dispersal can come from either an external species pool as in the island biogeography theory (MacArthur and Wilson 1967) or occupied patches inside the meta-community as in the meta-population theory (Levins 1969). In most ecosystems, dispersal is a mixture of both: forest plots receive seeds generated both within and outside the plot (Clark et al. 1999); human gut microbiomes come from common food/water sources (David et al. 2014) and from interactions with other people (Bashan et al. 2016). Whether the two types of dispersal create different beta diversity–dispersal relationships is unclear. I hypothesize that the mainland–island dispersal is more likely to lead to community homogenization than the meta-population dispersal because a constant external species pool increases the number of widespread species.

Disturbance has been observed to interact with dispersal to produce non-negative beta diversity–dispersal relationship (Lepori and Malmqvist 2009, Catano et al. 2017, Ojima and Jiang 2017). One hypothesis is that in the presence of disturbance, locally adapted species will be favored compared to widespread species hence increasing community divergence because of stronger selection (Questad and Foster 2008). An alternative hypothesis is that, due to the stochastic nature of disturbance, community divergence can be achieved by reducing the prevalence of widespread species (Myers et al.

2015). Therefore, I expect that dispersal is more likely to result in community divergence when disturbance becomes more intense.

Biotic interactions have always played an important role in shaping beta diversity. Different types of biotic interactions have different impacts on beta diversity–dispersal relationships. For example, in the competition–colonization trade-off (Tilman 1994, Hanski 2008), equally increasing the dispersal rates of all species increases the strength of regional niche-selection and will ultimately eliminate the inferior competitors and lead to community homogenization (Thompson et al. 2020); In predator–prey dynamics, increasing dispersal can lead to community divergence by the introduction of generalist predators due to more stochastic extinctions (Ryberg et al. 2012) or lead to community homogenization if predators specializes on uncommon prey species and enhances deterministic selection (Chase et al. 2009). Positive biotic interactions such as facilitation can lead to community divergence if the occurrence of the dominant species is suppressed by the facilitation of uncommon species (McIntire and Fajardo 2014, Ballantyne and Pickering 2015, Vega-Álvarez et al. 2019).

Lastly, environmental heterogeneity (Gianuca et al. 2017), habitat connectivity (Hewitt et al. 2005, Suzuki and Economo 2021) and functional diversity of the species pool (Patrick and Brown 2018) can also modify the beta diversity–dispersal relationship: if the strength of niche-selection increases with dispersal, a homogeneous landscape will select for the most suitable species across patches (Ron et al. 2018), while a heterogeneous landscape will select for divergent communities if there are enough inter-specific variations in the species pool; the structure of spatial networks can also have a profound effect by mediating the shifts between species sorting and mass effect meta-community archetypes (Suzuki and Economo 2021).

In summary, the one-sided story of 'dispersal leads to community homogenization' might impede our ability to predict biodiversity change as human-facilitated dispersal becomes more and more common (Bullock et al. 2018). To find out how dispersal could lead to different beta diversity changes necessitates a bottom-up theoretical investigation of the governing principles. To progress toward this goal, I illustrate the key drivers of the beta diversity–dispersal relationships through stochastic colonization and extinction dynamics in occupancy-based models. Specifically, I expect that increasing dispersal is more likely to result in community divergence when: 1) meta-population type dispersal rather than mainland–island type dispersal is at play; 2) disturbance is high in the meta-community; 3) biotic interactions are strong.

Material and methods

I begin with simple two-species occupancy models to illustrate the mechanism of the emergence of non-negative beta diversity–dispersal relationship through mathematically tractable systems. I then extend the investigation to a spatially explicit meta-community with multiple species and multiple islands using a discrete Markov model (Cazelles et al. 2016). I use Jaccard dissimilarity for measuring beta diversity following a previous study on island biogeography theory (Lu et al. 2019). The results obtained from the Jaccard dissimilarity are robust to the use of other occupancy-based beta diversity metrics such as Sorensen and Whittaker's beta diversity (Whittaker's beta in Supporting information), because they are monotonic transformations of the effective beta diversity (Chao et al. 2016).

The two-species models

Consider two identical islands where the occurrence probability of species 1 on each island is p and the occurrence probability of species 2 is q. By assuming that species' occurrences are independent, I can calculate the occurrence probability of each meta-community state as well as its associated beta diversity. For example, the probability of species 1 present on island 1 but absent on island 2, and species 2 present on island 2 but absent on island 1, is $p(1-p)q(1-q)$. The Jaccard dissimilarity between the two islands is 1 since no species is shared between islands. The expected Jaccard dissimilarity is calculated as (see derivation in Supporting information and graph of Eq. 1 in Fig. 1A):

$$E\left(\text{Jaccard.dissimilarity}\right) = \frac{2\left(q-1\right)q + p\left(4q-2-3q^2\right) + p^2\left(2-3q+2q^2\right)}{p^2\left(q-1\right)^2 - 2p\left(q-1\right)^2 + \left(q-2\right)q} \tag{1}$$

When $q=0$ or $p=q$, Eq. 1 becomes:

$$E\left(\text{Jaccard.dissimilarity}\right) = \frac{2\left(1-p\right)}{2-p} \tag{2}$$

When $q=1$, Eq. 1 becomes:

$$E\left(\text{Jaccard.dissimilarity}\right) = p\left(1-p\right) \tag{3}$$

In the island biogeography model, immigrant species only come from the mainland species pool (MacArthur and Wilson 1967). The occurrence probability of a species on an island is a function of extinction rate e and colonization rate c:

$$\frac{dp}{dt} = c\left(1-p\right) - ep \tag{4}$$

The equilibrium occurrence probability is:

$$p = \frac{c}{c+e} \tag{5}$$

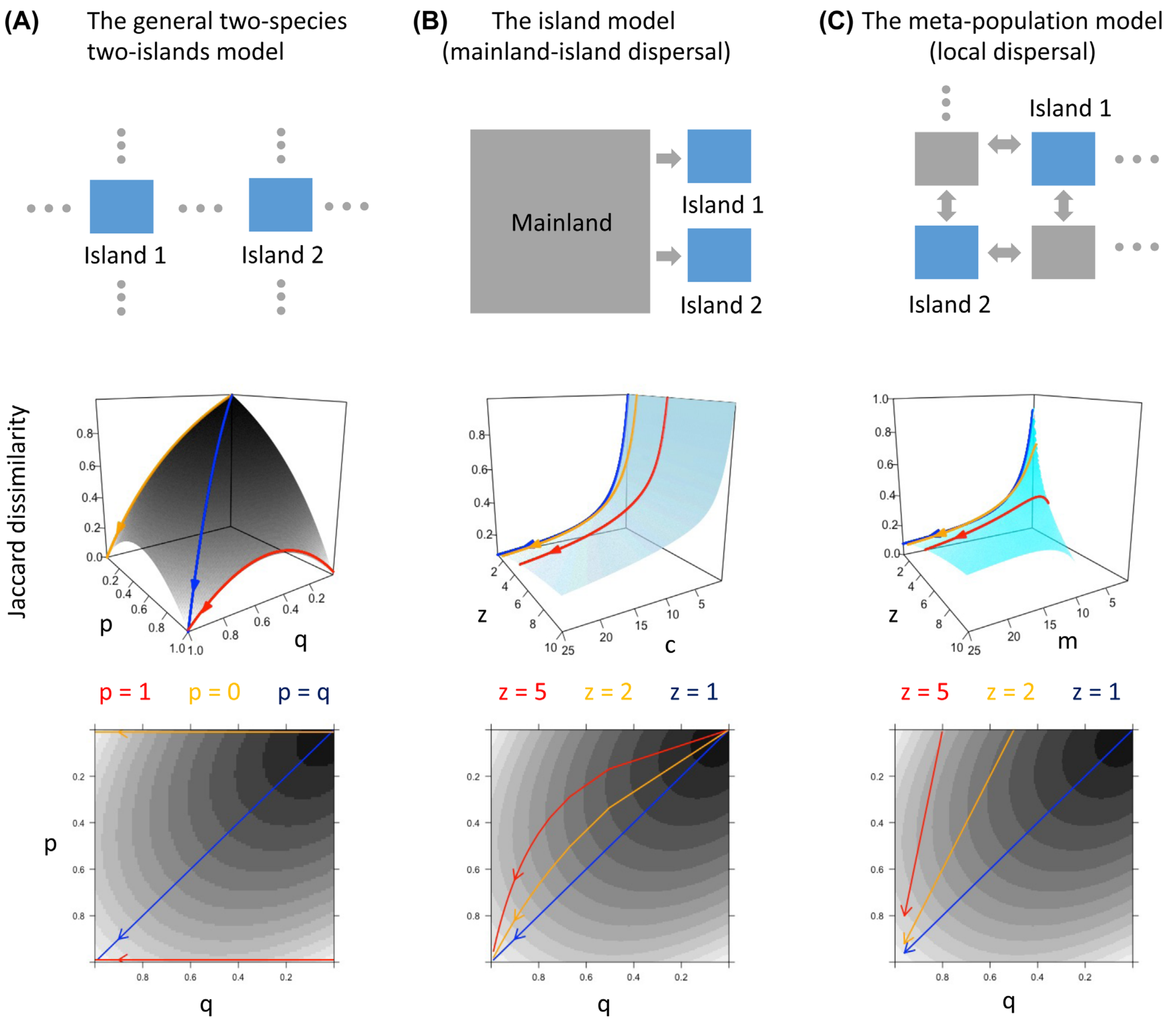

Figure 1. Two-species models with independent occurrences. Extinction rates are set to 1. (A) Relationship between Jaccard dissimilarity and the occurrence probability of species 1 (p) and species 2 (q) in the general two-species model (Eq. 1). Occurrence probability on an island can be interpreted as the number of times a species will be found when the island is sampled for a duration of time. A negative beta diversity–dispersal relationship arises when dispersal equally increases p and q, or when $q = 0$ and dispersal only increases p (Eq. 2) A hump-shaped beta diversity–dispersal relationship arises when $q = 1$ and dispersal only increases p (Eq. 3). (B) Relationship between Jaccard dissimilarity and mainland dispersal rate (c) and deviation from species-equivalent assumption (z) in the island model. Beta diversity only decreases with dispersal in the island biogeography model. (C) Relationship between Jaccard dissimilarity and local dispersal rate (m) and deviation from species-equivalent assumption (z) in the meta-population model. A hump-shaped beta diversity–dispersal relationship arises when z is large. The island model (B) and the meta-population (C) model are both derived from the general model (A) by assuming different occurrence probability–dispersal relationships. Arrows show the trajectories of the beta diversity–dispersal relationships under different scenarios. The bottom row shows the trajectories on the contour maps of the general two-species model (A).

Assuming equivalence between two species, and substituting (5) into Eq. 2, the expected Jaccard dissimilarity becomes:

$$E\left(\text{Jaccard.dissimilarity}\right) = \frac{2e}{2e + c} \qquad (6)$$

For the non-equivalent case, let

$$p = \frac{c}{c + e}$$

and

$$q = \frac{c}{c + ze}$$

z is the ratio of extinction rates between species 2 and species 1, which models the deviation from the species-equivalent assumption. z can also be interpreted as a measure of relative sensitivity to disturbance. Without loss of generality, the extinction rate is set to 1 to examine the beta diversity–dispersal relationship.

The meta-population model assumes that there are infinite number of patches, all patches are equally connected and there is no external immigration (Levins 1969). The meta-population theory models the occupancy frequency as a function of extinction rate e and immigration rate m:

$$\frac{dp}{dt} = mp\left(1-p\right) - ep \tag{7}$$

At equilibrium, the occupancy frequency becomes:

$$p = 1 - \frac{e}{m} \tag{8}$$

The occurrence probability of a species on any island equals the occupancy frequency at equilibrium. Substituting (8) into Eq. 2, the expected Jaccard dissimilarity becomes:

$$E\left(\text{Jaccard.dissimilarity}\right) = \frac{2e}{e+m} \tag{9}$$

For the non-equivalent case, let

$$p = 1 - \frac{e}{m}$$

and

$$q = 1 - \frac{ze}{m}$$

where z has the same interpretation as in the island biogeography model.

The multiple-species models

To extend the result in Eq. 1 to a multiple-species model, I first draw the occurrence probability of species i from a uniform distribution: $p_i \sim \text{unif}(p_{\min}, p_{\max})$. The minimum and maximum occurrence probabilities are varied along a hypothetical dispersal gradient to create different combinations of the variance and the mean of species-level occurrence probabilities. Then I simulate the community matrices (in a community matrix, 0 indicates absence and 1 indicates presence; rows represent islands and columns represent species) 1000 times and calculate the mean Jaccard dissimilarity.

To further take biotic interactions and local dispersal into account, I use a discrete Markov model for meta-community simulations (Cazelles et al. 2016). The stationary distribution of the meta-community is determined by the extinction and colonization probabilities.

The extinction probability of species i on island x, following Cazelles and colleagues (2016) is:

$$f_{ix} = \frac{1}{1+\left(\frac{1}{e_{ix}}-1\right)\exp\left(d\sum_{j\neq i}^{S} a_{ij}O_{jx}\right)} \tag{10}$$

Where e_{ix} is the baseline extinction probability of species i on island x when there is no biotic interactions; a_{ij} is an interaction coefficient which models the effect of species j on species i (negative implies suppression, positive implies facilitation), d is a scaling constant to control the average interaction strength; O_{jx} is the occurrence of species j on island x (1 for presence, 0 for absence); and S is the total number of species in the species pool. The extinction probability f is a sigmoid function of the total interaction: positive interactions decrease the extinction rate of species i, while negative interactions increase the extinction rate of species i (Cazelles et al. 2016).

To calculate the colonization probability, I assume that an empty island x can be colonized either by mainland immigrants or immigrants from other occupied islands. I also assume constant colonization rate from the mainland and that inter-island colonization is a function of local dispersal rate, island connectivity and island occupancies. Under the assumption that the number of emigrants from an island follows a Poisson distribution and all islands have the same carrying capacity, the probability of having no immigrants from other islands is $\exp\left(-m\sum_{y\neq x}^{n} h_{yx}O_{iy}\right)$, where m is the local dispersal rate, n is the total number of islands, h_{yx} is the connectivity of island y to island x and O_{iy} is the occurrence of species i on island y. The probability of having no immigrants from the mainland is $1 - c_i$, where c_i is the mainland colonization rate. Then the colonization probability g_{ix} is the probability of at least one immigrant either from the mainland or from other islands arrive at the focal island:

$$g_{ix} = 1-\left(1-c_i\right)exp\left(-m\sum_{y\neq x}^{n} h_{yx}O_{iy}\right), \tag{11}$$

The simulation starts with a random community matrix in 0s and 1s, with rows representing islands and columns representing species. At each time step, I do the followings:

1) Calculate the extinction probability and colonization probability of each species at each island according to Eq. 10 and 11.
2) Simulate the community matrix at the next time step with the calculated extinction and colonization probabilities.
3) Calculate the mean pairwise Jaccard dissimilarity with the new community matrix using the R package 'betapart' (Baselga et al. 2021).

I iterate the community matrix with 2000 steps and take the mean Jaccard dissimilarity of the last 100 iterations as the expected Jaccard dissimilarity for the meta-community. Equilibrium for alpha, beta and gamma diversities are generally reached within 1000 iterations (Supporting information).

Parameter settings

50 species and 9 islands are used to simulate the multiple-species model. Islands are laid out as a 3 by 3 grid lattice. The connectivity h_{xy} among islands in Eq. 11 is calculated as a negative exponential function of their distances: $h_{xy} = \exp[-\text{distance}(x,y)]$. The interaction strength is controlled by d, with $d = 0$ indicating no interaction and $d = 0.01$, $d = 0.1$, $d = 1$ corresponding to different levels of interaction intensity. For generality, the interactions coefficients among 50 species are randomly drawn from a uniform distribution $a_{ij} \sim \text{unif}(-5,0)$. This assumes that all kinds of competition including asymmetric and intransitive competitions are allowed. More exclusive types of competition produce similar results which are not shown. For beta diversity–local dispersal relationship, I use two levels of mainland dispersal rate ($c = 0.001$ and $c = 0.1$) and three levels of baseline extinction rates by randomly drawing from a uniform distribution: $e_i \sim \text{unif}(0.01, 0.02)$, $e_i \sim \text{unif}(0.1, 0.2)$ and $e_i \sim \text{unif}(0.8, 0.9)$. For beta diversity–mainland dispersal relationship, I use two levels of local dispersal rate ($m = 0$ and $m = 0.1$) and the same levels of baseline extinction rates described above. I also examine whether the results are robust to a random interaction network (which includes both positive and negative interactions), different environmental heterogeneity and niche breadth, Whittaker's beta diversity, size of the species pool, interspecific variations in mainland dispersal rates in the Supporting information.

The null model

Lastly, to assess whether the beta diversity–dispersal relationship is generated by changes in species-level occurrence probabilities alone, I calculate the beta diversity from a null model where the marginal occurrence probabilities of species on each island (estimated from the last 100 iterations of the Markov chains) are used to simulate community matrices. The mean and the standard deviation of the null beta diversity is calculated from 1000 simulated community matrices. The null model assumes that species' occurrences are independent from each other conditioning on given marginal occurrence probabilities. I also calculate the standardized Jaccard dissimilarity by subtracting the mean and dividing by the standard deviation of the null model.

Results

The two-species models

In the general two-species model, if we assume that species 2 is nearly absent ($q = 0$) and dispersal only increases the occurrence probability of species 1 p, beta diversity will only decrease with dispersal (Eq. 2; Fig. 1A). If we assume that dispersal equally increases the occurrence probabilities of species 1 and species 2 ($p = q$), beta diversity will also decrease with dispersal (Eq. 2; Fig. 1A). However, if species 2 is always present ($q = 1$), beta diversity will be a quadratic function of dispersal (Eq. 3; Fig. 1A).

Therefore, in both the island biogeography model and the meta-population model, species-equivalent assumption will always produce negative beta diversity–dispersal relationships (Eq. 6, 9; Fig. 1B–C). A hump-shaped beta diversity–dispersal relationship will only arise in the meta-population model when species 1 and species 2 become significantly different (Fig. 1C). Using Whittaker's beta diversity produces similar results (Supporting information).

The multiple-species models

When generalized to a multiple-species model, the results of the two-species model can be more clearly understood in terms of the variance and the mean of species-level occurrence probabilities. If dispersal decreases the variance of the species-level occurrence probabilities but does not change the mean occurrence probability, beta diversity will increase with dispersal (Fig. 2A). If dispersal decreases the variance but slightly increases the mean of the occurrence probabilities, a hump-shaped beta diversity–dispersal relationship will arise (Fig. 2B). If mean occurrence probability increases more rapidly, beta diversity will only decrease with dispersal (Fig. 2C).

Using a spatial explicit meta-community model, I show that a hump-shaped beta diversity–dispersal relationship only arises when meta-population type dispersal is present, biotic interactions are strong and mainland dispersal rate is low (Fig. 3A–C). Mainland dispersal only has a homogenizing effect except for when meta-population dispersal is present (Fig. 3J–K). Moreover, the beta diversity–dispersal relationship is mainly driven by the changes in species-level occurrence probabilities as shown by the null model (dashed lines in Fig. 3). The standardized beta diversity in most cases is not significantly different from 0 (within the ± 1.96 95% confidence intervals: Fig. 4). These results are robust to a random interaction network, different environmental heterogeneity, niche breadths, the use of Whittaker's beta diversity, size of species pool and interspecific variations in mainland dispersal rates (Supporting information).

Discussion

Theoretical results

Using occupancy-based meta-community models, I show that different beta diversity–dispersal relationships (e.g. positive, negative and hump-shaped) can be generated by the changes in species-level occurrence probabilities alone. Specifically, when the mean occurrence probability is fixed, a decreasing variance of species-level occurrence probabilities will lead to higher beta diversity (Fig. 2A); when the

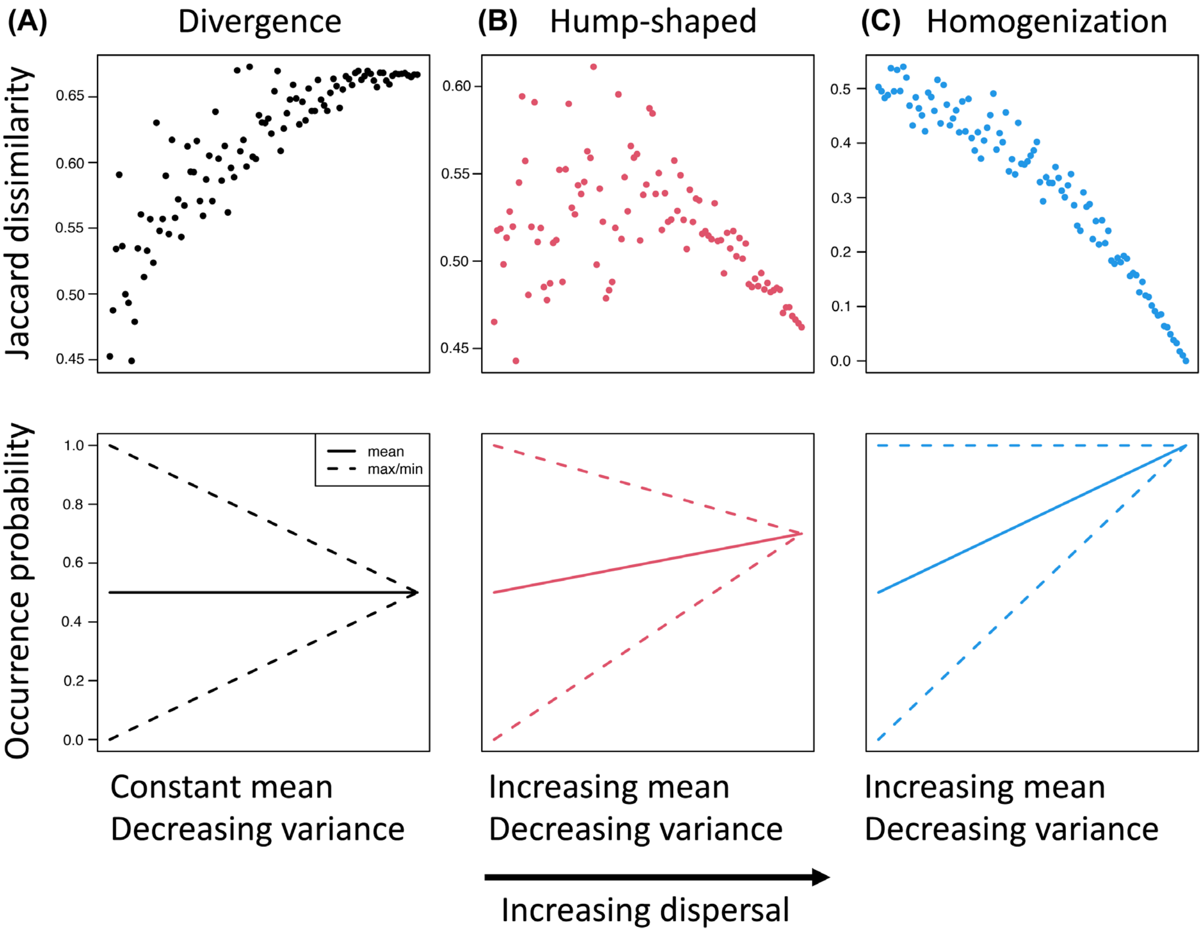

Figure 2. Effects of the variance and the mean of species' occurrence probabilities on beta diversity for a general multiple-species model assuming independent occurrence. 50 species and 9 islands are used for the simulation. Species occurrence probabilities are randomly drawn from a uniform distribution. The minimum and maximum values of the uniform distributions are artificially varied along a dispersal gradient to create different combinations of the variance and the mean of occurrence probabilities. Solid lines show the mean occurrence probabilities, dashed lines show the maximum and minimum values of the uniform distribution. Community matrices are simulated from the drawn occurrence probabilities. The mean Jaccard dissimilarity of 1000 simulations are shown. (A) When increasing dispersal does not change the mean but reduces the variance of occurrence probabilities, a positive beta diversity–dispersal relationship will arise. (B) When increasing dispersal slightly increases the mean and reduces the variance, a hump-shaped beta diversity–dispersal relationship will arise. (C) When increasing dispersal increases the mean and reduces the variance, a negative beta diversity–dispersal relationship will arise if the effect of an increasing mean occurrence probability is stronger.

variance of occurrence probabilities is fixed, an increasing mean occurrence probability will lead to lower beta diversity (Lu et al. 2019). A positive or hump-shaped beta diversity–dispersal relationship will arise when the effect of decreasing variance is stronger than the effect of increasing mean (Fig. 2B). This could be understood heuristically from the relationship between beta diversity, alpha diversity and gamma diversity: $\beta=\gamma/\alpha$ (Whittaker 1960, Chao et al. 2016). In a meta-community of k islands and n species, if the occurrence probability of species i on each island is p_i and species' occurrence are independent on each island, then the expected gamma diversity is $\sum_{i=1}^{n}\left[1-\left(1-p_i\right)^k\right]$ and the expected alpha diversity is $\sum_{i=1}^{n} p_i$. When the mean occurrence probability is fixed (equivalent to fixing the alpha diversity), the gamma diversity and beta diversity are maximized when $p_1=p_2=\ldots=p_n$. Therefore, the only way to generate a positive or hump-shaped beta diversity–dispersal relationship when mean occurrence probability (alpha diversity) increases is by reducing the variance of occurrence probabilities. More generally, as long as gamma diversity increases faster than alpha diversity, a positive beta diversity–dispersal relationship will arise. This is consistent with the findings in the nectar microbe experiment (Vannette and Fukami 2017), and a competition–colonization trade-off meta-community model (Thompson et al. 2020) and also explains why the neutral model (Hubbell 2001) and species-equivalent island biogeography model (Lu et al. 2019) only predict a negative beta diversity–dispersal relationship.

I have given a statistical explanation of how a positive or hump-shaped beta diversity–dispersal relationship could arise. However, a more challenging task is to find out what assembly processes could reduce the variance of occurrence probabilities

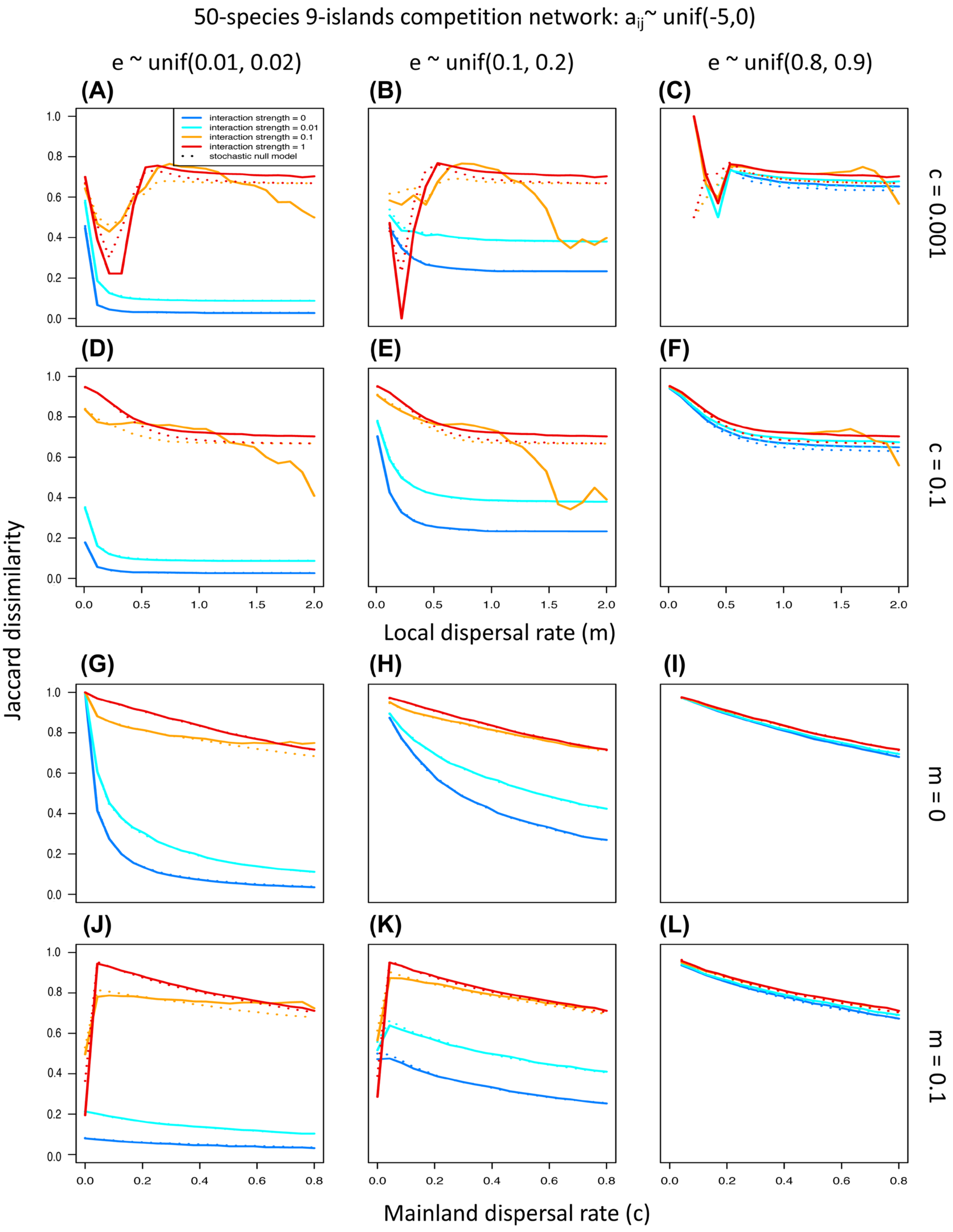

Figure 3. (A)–(F) Relationship between Jaccard dissimilarity and local dispersal rate in the 50-species 9-islands meta-community model with a competition network where interaction coefficients are drawn from a uniform distribution: a_{ij} ~ unif(−5,0). (G)–(L) Relationship between Jaccard dissimilarity and mainland dispersal rate in the 50-species 9-islands meta-community model with a competition network. Dashed lines show the results of a null model where beta diversity is estimated from the observed marginal occurrence probabilities.

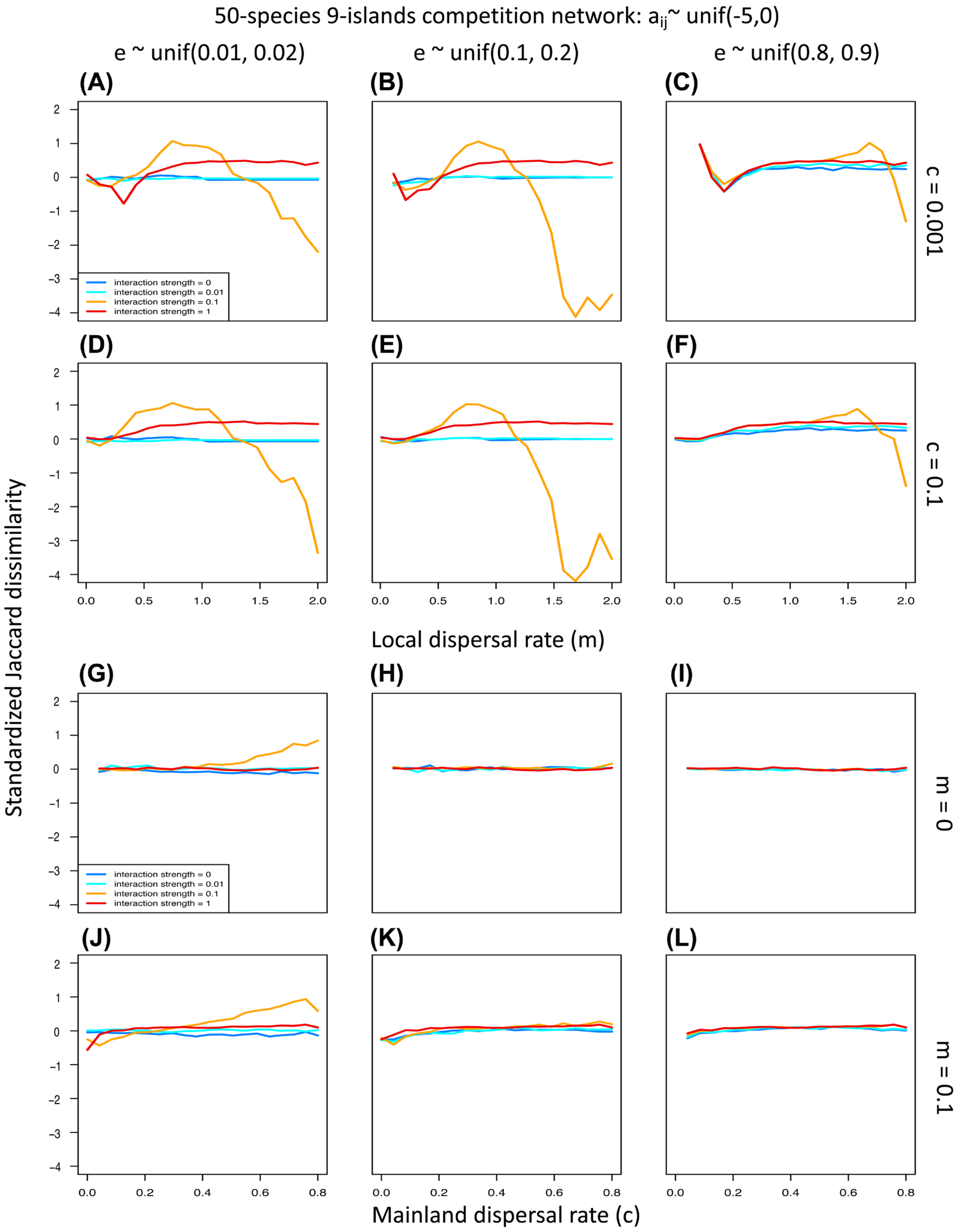

Figure 4. Standardized Jaccard dissimilarity (calculated as the observed mean subtracted by the mean and divided by the standard deviation of the null model) with increasing dispersal rates for the 50-species competition model.

with more dispersal. I identified three important factors in this paper: meta-population dispersal (rather than mainland–island dispersal), disturbance and strong biotic interactions.

The meta-population model mainly differs with the island biogeography model in its occupancy-dependent assumption of dispersal (Eq. 7). Under this assumption, the occurrence probability of the rare species increases faster with dispersal than the widespread species, therefore reducing the variance of occurrence probabilities (Fig. 1C). Strong biotic interactions are also capable of reducing the variance of occurrence probabilities by suppressing the occurrence probability of the dominant species (Supporting information) but only create hump-shaped patterns in the presence of meta-population dispersal (Fig. 3). This is consistent with the findings of the nectar microbe experiment (Vannette and Fukami 2017) and the competition–colonization trade-off meta-community model (Thompson et al. 2020). Lastly, disturbance is important in creating stochastic extinctions in the meta-community, which prevents the dominance of a single species in a homogeneous environment (Ron et al. 2018). The intensity of disturbance might also be important in reducing gamma diversity in the absence of dispersal, therefore creating room for a positive beta diversity–dispersal relationship (note that beta diversity can only decrease when the meta-community is saturated by the species pool). This might explain why a non-negative beta diversity–dispersal relationship was mostly observed in experiments with disturbance settings (Questad and Foster 2008, Lepori and Malmqvist 2009, Catano et al. 2017, Ojima and Jiang 2017).

In this paper, I only examined the effect of stochastic extinction and colonization in occupancy-based meta-community models. However, it is unclear how abundance-based beta diversity will respond to dispersal when density-dependent factors are considered. Further studies on abundance-based models (such as in Thompson et al. 2020) are needed to understand how will demographic stochasticity and density-dependent mechanisms affect the beta diversity–dispersal relationship.

Implications for empirical studies

My findings suggest that stochastic meta-population dispersal is a key driver of the positive beta diversity–dispersal relationship. The commonly used 'merge and redistribute' dispersal technique in most microcosm experiments eliminates the stochasticity in the number of patches can be reached by the immigrants, thus allowing only abundance variations in generating beta diversity (Grainger and Gilbert 2016). However, such stochasticity is very common in the real world especially when dispersal is facilitated by animal movements (Bowler and Benton 2005), winds (Tackenberg 2003) and human transportations (Banks et al. 2015). As many concerns over dispersal address the problem of habitat fragmentation (Jamoneau et al. 2012) and human-facilitated dispersals through roads, livestock and vehicles (Auffret et al. 2014, Bullock et al. 2018), stochasticity as to where and when colonization can happen is essential to predict biodiversity change. Therefore, I advocate that more experiments mimicking natural dispersal conditions, such as in Vannette and Fukami's (2017) nectar microbes, are needed to fully understand how dispersal impacts biodiversity.

Biotic interactions are also critical for the emergence of positive beta diversity–dispersal relationship. However, the effect of biotic interactions on beta diversity cannot always be detected by a randomized null model (Fig. 4), especially when biotic interactions strongly affect the marginal occurrence probabilities of species. Because accounting for the dependence of beta diversity on mean occurrence probability or alpha diversity will remove the effect of interest and decrease the statistical power (Vellend et al. 2014, Ulrich et al. 2017, Šizling et al. 2021).

At last, I advocate a more careful consideration of the system (and preferably explicit parameterization) when studying the effect of dispersal. As a closed system and an open system can create different beta diversity–dispersal relationships. An advantage of the occupancy-based models is that they can be easily parameterized into a dynamic multiple-species occupancy model by modeling the probabilities of extinction and colonization and to generate predictions for biodiversity changes (Fidino et al. 2019, Ontiveros et al. 2019, Riddell et al. 2021).

Conclusions

Using occupancy-based meta-community models, I show that many possible relationships between beta diversity and dispersal can arise through changes in species-level occurrence probabilities alone. The emergence of a positive beta diversity–dispersal relationship is closely related to a decreasing variance of occurrence probabilities created by meta-population dispersal, disturbance and strong biotic interactions. These findings highlight the intrinsic constraints of the variance and the mean of species-level occurrence probabilities on beta diversity changes; and motivate future experiments on more realistic dispersal manipulations and detailed understanding of the interaction network in the studied system to test beta diversity–dispersal relationships.

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Data availability statement

This study does not contain empirical data. The codes for reproducing the simulations are available from Zenodo: <https://zenodo.org/record/5469920>. (Lu 2021).

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