

## Chapter 4

# Effects of Metacommunity Networks on Local Community Structures: From Theoretical Predictions to Empirical Evaluations

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## INTRODUCTION

Significant losses of species, homogenization of biotas, changes in climatic conditions, and reduction or fragmentation of ecosystems will likely occur through the current century (D'Antonio et al., 2001; May et al., 1995; Scheffer et al., 2009). In addition to the direct effect on biodiversity, several ecosystem processes that support human societies will be impacted (Loreau, 2010; Nicholson et al., 2009). The discipline of ecology will have a central role in this changing world by accounting for mechanisms involved in these ongoing processes (Loreau, 2010; Loreau et al., 2001). Ecological theory has focused primarily on local determinants of species coexistence as a main approach to explaining biodiversity patterns (Diamond, 1975; Gotelli et al., 1997; MacArthur, 1970; MacArthur and Levins, 1964, 1967). At the same time, Lotka–Volterra models and small-scale experiments with few species have dominated the literature (Hutchinson, 1959; MacArthur and Levins, 1964; Pianka, 1974; Ritchie, 2010). In spite of the significant advances achieved by these approaches (Chase and Leibold, 2003; Chesson, 2000), they alone do not account for biodiversity patterns and functions across diverse ecological and evolutionary scales (Maurer, 1999; Morin, 2010; Ricklefs and Schluter, 1993). In consequence, new theoretical and

methodological approaches to the study of biodiversity have emerged in recent decades.

A groundbreaking set of novel theories with new methodologies and a focus on alternative mechanisms has been formulated in recent years (Ritchie, 2010; p. 199). Among them, we emphasize the unified neutral theory of biodiversity and biogeography (Hubbell, 2001; Rosindell et al., 2011), the metabolic theory of ecology (Brown et al., 2004), the spatial scaling law (Ritchie, 2010), and two theories based on maximum entropy (MaxEnt) formalisms (Harte, 2011; Shipley, 2010a). To some extent, macroecology, with its focus on basic principles structuring biodiversity, prepared the groundwork for these new theories (Brown and Maurer, 1989). Perspectives such as those embedded in the neutral theory avoid considerations of niche-based processes and helped in the formulation of a novel synthesis of niche theory (Chase and Leibold, 2003). With such a plethora of new ideas, a search for unified theories combining some or all of them and unifying new theories with more classic concepts has become the holy grail of ecology (Chase, 2005; McGill, 2010). The discipline of metacommunity ecology may provide a framework for the unification of the different theories.

Metacommunity concepts have a long history in the science of ecology (Chase and Bengtsson, 2010); they represent natural extensions of the metapopulation approach to multispecies systems (Hanski and Gilpin, 1991; Loreau, 2010). The metacommunity concept connects primary biogeographical and community theories, such as those relating to species co-occurrences among communities (Holt, 1997; Leibold and Mikkelsen, 2002; Ulrich and Gotelli, 2007), the link between local and regional diversity (Holt, 1993), and the neutral theory of ecology, which considered metacommunity–community immigration as a basic determinant of community structure (Hubbell, 2001). Some of the most important contributions to biological thinking have emerged in the introduction of new concepts (Mayr, 1997). There is no doubt that the metacommunity concept, together with the growing formalization of related theories, is producing important changes in the discipline of community ecology. Local communities are no longer considered isolated units in which local processes determine their structure and function (Baiser et al., 2013; Brown and Swan, 2010; Carrara et al., 2012; Loreau et al., 2003; Moritz et al., 2013). The theoretical and empirical evidence available indicates that the effects of large-scale processes on community structure and diversity may be equally as important as or more important than long-studied local determinants (Borthagaray et al., 2012; Economo and Keitt, 2008; Leibold et al., 2004; Mouquet and Loreau, 2003). Furthermore, the classic local–regional dichotomy might well be an oversimplification (Cadotte, 2006).

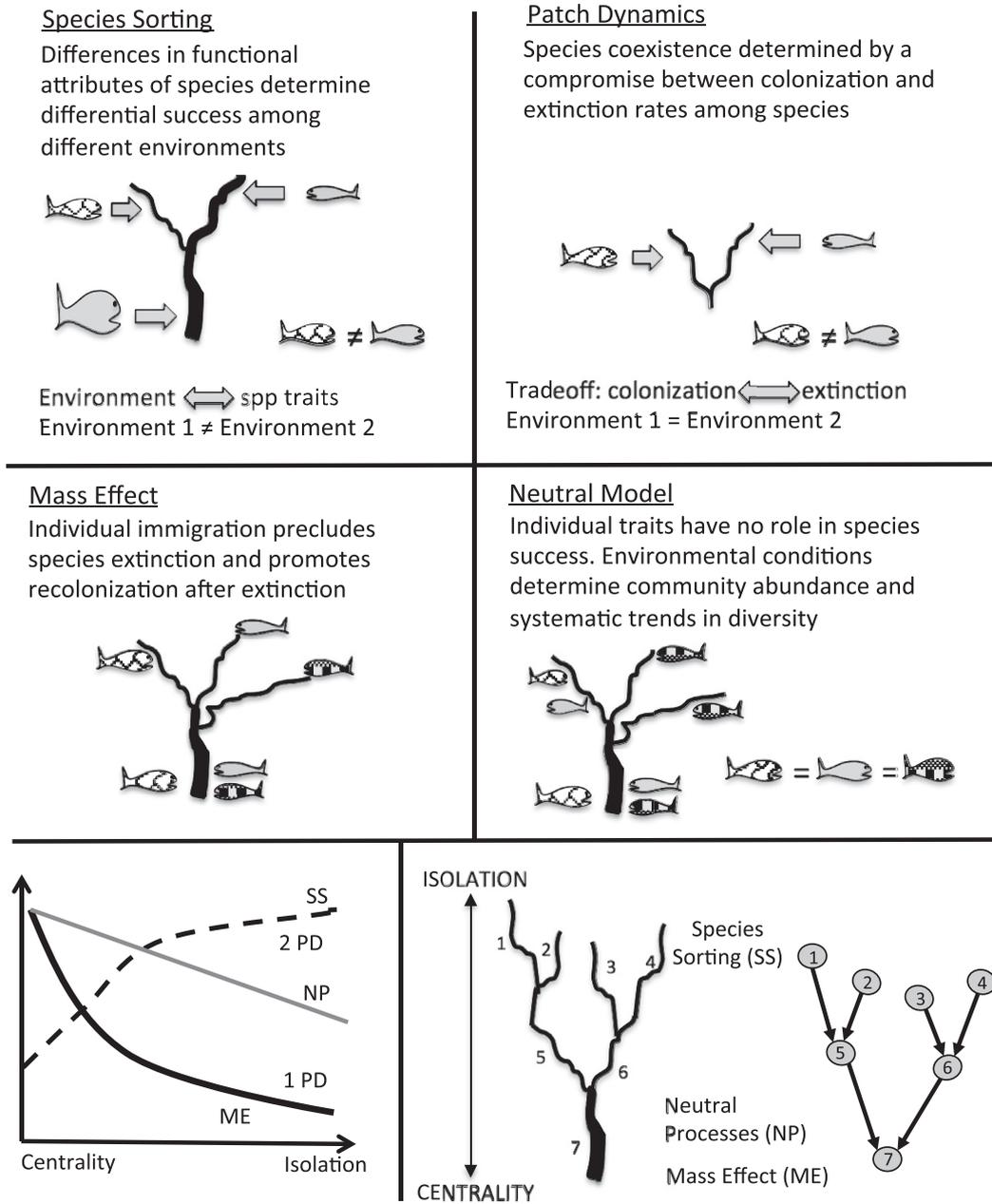
Dissociation between theoretical predictions and their empirical evaluation is a chronic problem in ecology (Abrams, 2001; Arim et al., 2007; Hanski, 1999). While foundational publications on ecological theories have been cited

thousands of times (e.g., [Leibold et al., 2004](#)), reports of their empirical testing are orders of magnitude fewer ([Logue et al., 2011](#)). Metacommunity ecology is rapidly advancing through theoretical considerations, but the empirical counterpart is in its infancy ([Baiser et al., 2013](#); [Dorazio et al., 2010](#); [Driscoll and Lindenmayer, 2009](#); [Logue et al., 2011](#)). In order to contribute to the construction of a strong theoretical framework, the empirical approach must be able to discriminate among potential mechanisms even when several of these drivers may seem to underlay observed patterns ([Platt, 1964](#)). Analyses of the purely neutral model, partitioning of variance, and site-by-species incidence matrices have been foci of interest in empirical evaluations of metacommunity theory ([Meynard et al., 2013](#)). Spatial autocorrelation in community compositions has also been used to analyze dispersal patterns ([Shurin et al., 2009](#); [Soininen et al., 2007](#)). [Baiser et al. \(2013\)](#) and [Dorazio et al. \(2010\)](#) have proposed additional new methods for empirical testing. Here, we argue that MaxEnt theory has a major role in the analysis of metacommunity mechanisms ([Shipley, 2010b](#); [Shipley et al., 2006](#)) and that graph theory provides a robust procedure for the quantification of metacommunity network structure and local community isolation. The use of graph theory for metacommunity studies has been emphatically recommended in recent years ([Altermatt, 2013](#); [Economio and Keitt, 2010](#); [Gonzalez et al., 2011](#); [Peterson et al., 2013](#)). However, the methods by which networks may be empirically determined are not always obvious; here, we review potential alternatives.

In this chapter we contribute to reducing the distance between metacommunity theory and empirical evaluation by reviewing predictions from metacommunity theory and proposing tools for their testing using field observational data. In the subsequent sections, we briefly introduce the main conceptual frameworks related to metacommunity theory. Following this introduction to mechanisms and predictions, we focus on methodological procedures for their evaluation.

## FOUR PARADIGMS

Outstanding reviews and presentations of metacommunity theory have been published previously ([Chase and Bengtsson, 2010](#); [Holyoak et al., 2005a](#); [Leibold et al., 2004](#)). Here, we highlight basic mechanisms and predictions that should be a focus of empirical analyses. We start by presenting four nonexclusive metacommunity paradigms: patch dynamics, mass effect, species sorting, and neutral dynamics (see [Figure 1](#)). The central message here is that a wide range of predictions emerges from metacommunity mechanisms, and closely similar predictions frequently arise from different theoretical mechanisms. In addition, analyzing the role of organismal traits in the assembly of communities and in environment–trait associations is crucial to the disentanglement of competing theoretical mechanisms predicting similar community patterns.



**FIGURE 1** Four nonexclusive metacommunity mechanisms. This example considers a fish metacommunity in a river. Fish patterns represent observed traits, and a different environment is assumed among river headers, and between headers and river mouths. Each box contains one of the four “paradigms” of metacommunity ecology: species sorting, patch dynamics, mass effect, and neutral processes. These paradigms are expected to systematically rise or decrease with community isolation. The trend in patch dynamics with isolation is contingent on the relative effects of isolation on dominant and subordinate competitors. The lower right side panel presents a graph representation of a river and the regions where the different mechanisms are expected to be more relevant.

## Patch Dynamics and Mass Effect

We focus here on two of the four main perspectives in metacommunity ecology: patch dynamics and mass effect. These mechanisms may be conceptualized by different analytical and conceptual approaches (Holyoak et al., 2005a). Among them, metapopulation theory has the advantage of connecting population ecology with biogeography and landscape ecology through simple and general models (Gotelli, 1991). We concentrate on the derivation of patch dynamics and mass effect from metapopulation models. This approach identifies basic mechanisms beyond each of the paradigms and provides further predictions on the potential operation of specific mechanisms along a gradient of community centrality—isolation (Figure 1).

Metapopulation models represent three contrasting scenarios of scale and ecological level. First, a model may represent the occurrence of populations across a landscape (Levins, 1969). Second, it may represent space occupancy by individuals from a single population (Tilman, 1994), and the model may have analogies to the logistic equation (Hanski, 1999). Third, a model may connect to the community level because the fraction of occupied patches is the probability that a species is present in a single patch. Assuming that species occurrences are mutually independent, as in the MacArthur and Wilson (1967) model, the expected richness in a local community is the product of species occurrence probability and the number of species in the regional pool (Gotelli, 1991; Hanski, 1999, 2010).

### *Patch Dynamics*

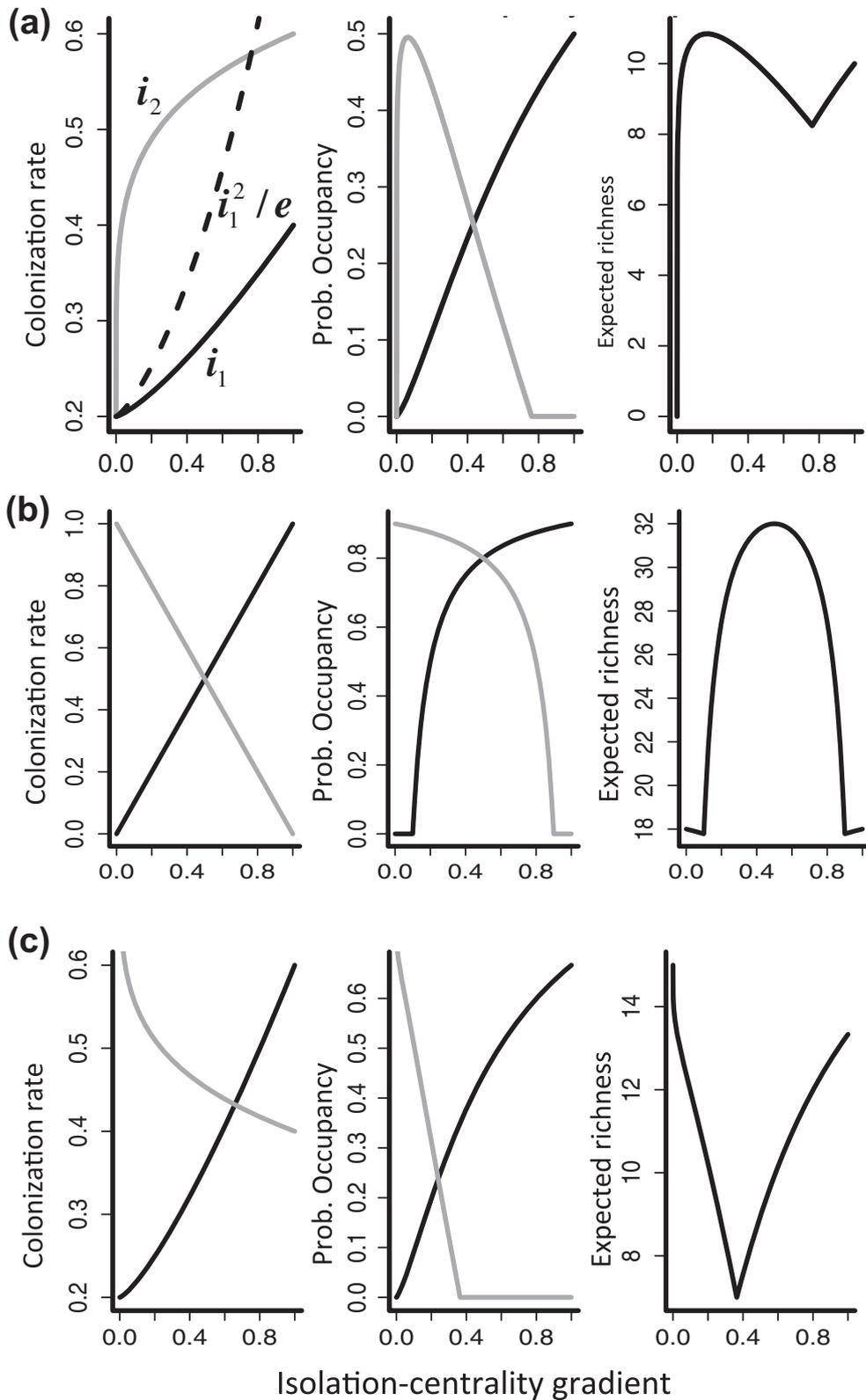
In a basic metapopulation model, local patches are colonized through immigration ( $i$ ) and evacuated through extinction ( $e$ ). The dynamics of occupied patches ( $P$ ) may be modeled as follows (Levins, 1969):

$$dP/dt = iP(1 - P) - eP \quad (1)$$

an expression implying that the fraction of occupied patches at equilibrium is  $P^* = 1 - e/i$ . A main consequence of this relationship is that no matter how good a species may be as a competitor, if it does not persist forever in a patch, a fraction of free environment will always remain unused.

It is instructive to consider the extreme example of one superior and one inferior competitor (Tilman, 1994). The superior competitor species always excludes the inferior one on arrival in a patch. The dynamics of the superior competitor species  $P_1$  are not affected by the presence in the landscape of the competitively inferior species:  $dP_1/dt = i_1P_1(1 - P_1) - e_1P_1$ . However, the inferior species experiences a reduction in the fraction of available habitat and an increase in local extinction once the superior competitor species arrives in the patch. The dynamics of the inferior competitor species  $P_2$  will be determined by:

$$dP_2/dt = i_2P_2(1 - P_1 - P_2) - e_2P_2 - i_1P_1P_2 \quad (2)$$



**FIGURE 2** Predictions of metapopulation models. Gray and black lines represent the trends in colonization rates and probabilities of patch occupancy of inferior and superior competitor species across an isolation gradient. (a): *Patch dynamic*—coexistence depends on the inferior competitors more rapidly capturing resources than the superior competitors. The dashed line represents the

which is a relationship implying that in order to maintain a positive population growth rate when the superior competitor species occupies its equilibrium proportion of the environment, the following relationship among demographic parameters should be satisfied:

$$i_2 > \frac{i_1(i_1 + e_2 - e_1)}{e_1} \quad (3)$$

When extinction rates are equal, the inequality simplifies to  $i_2 > i_1^2/e$ . This inequality implies that coexistence depends on the inferior competitor species having a faster rate of empty patch colonization, an outcome that may be generalized to many species (Tilman, 1994). This constraint is relaxed when the mortality rate of the inferior competitor species is lower than that of the superior competitor species, and the reverse is also true. These relationships determine patch dynamics in which species coexistence depends on a trade-off between species' rates of empty patch colonization versus species' abilities to colonize and defend a patch from future immigrants (Holyoak et al., 2005b).

In general, the combination of demographic parameters of inferior and superior competitor species should ensure that the former may persist in the patches left empty by the latter. The proportion of free patches for colonization when the superior competitor species is at equilibrium is:  $1 - \hat{P} = 1 - 1 + e_1/i_1 = e_1/i_1$ . Community isolation is considered to be a direct determinant of the rate of individual arrival and, consequently, of the colonization rate  $i$  (Altermatt, 2013; Economo and Keitt, 2010; MacArthur and Wilson, 1967). Since an isolation gradient determines an immigration gradient, more isolated communities should have reduced colonization rates. Patch dynamics involve inferior competitor species with enhanced dispersal abilities. The reduction in colonization rate among increasingly isolated patches should be greatest among better competitors, thus determining a reduction in the proportion of patches occupied by the dominant species (Figure 2(a)). The relative increase in the inferior species colonization rate in comparison with the superior competitor species rate relaxes the constraint of Eqn (1). In addition, free space should also foster opportunities for isolated patch specialist species. As a consequence, the more isolated a community is, the more opportunities there are for the

constraint  $i_2 > i_1^2/e$ , assuming equal extinction rates. Two pools of 10 dominant and 10 subordinate species are considered. A large turnover between subordinate and dominant species is expected. (b): *Species mixing*—a pool of isolation-specialists and a pool of central patch species are considered. Each species pool follows Levins dynamics with equal extinction rates but inverse trends in colonization with increasing community isolation. The coexistence of species from the two pools at intermediate isolation levels determines a humped pattern of diversity. (c): Similar to (b), but isolation-specialists are competitive subordinates. The more rapid decrease in the probability (Prob.) of isolation-specialist occurrence may determine minimum richness at intermediate isolation levels.

operation of patch dynamics. However, this trend may reverse if superior competitor species are able to reach more distant patches; for example, if those with large body sizes are able to travel longer distances between patches (Arim et al., 2010; Borthagaray et al., 2012; McCann, 2012). The propensity for patch dynamics in isolated communities (in contrast to the mass effect described below) is a main prediction of metacommunity theory (Brown and Swan, 2010). Metapopulation models emphasize the dependence of the main predictions of functional attributes present in the species pool (e.g., specialists in isolated environments) and/or the differential effect of isolation on the immigration rates of superior and inferior competitors.

### *Mass Effect*

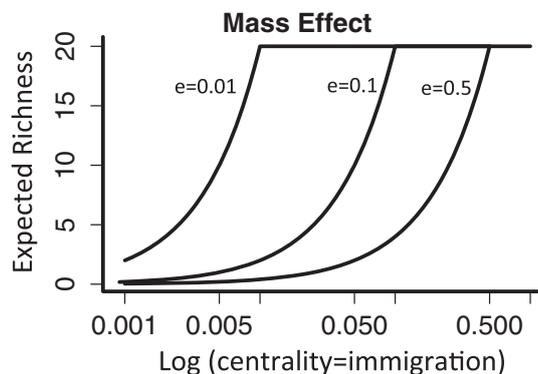
Metapopulation models also permit evaluation of expected trends in the role of an additional metacommunity mechanism, the “mass effect.” The individual flow from “source” populations in suitable environments to “sink” populations in less propitious environments may enhance species persistence under unfavorable conditions (Hanski, 1999; Shmida and Wilson, 1985). This source–sink dynamic may determine a rescue effect, whereby immigration prevents species extinction (Brown and Kodric-Brown, 1977). Even when extinction takes place, the inflow of individuals promotes a rapid colonization and persistence of the species in the environment. The enhanced species viability and community richness promoted by source–sink dynamics and rescue effects determine the second metacommunity mechanism termed “mass effect” (Holyoak et al., 2005a; Shmida and Wilson, 1985).

One advantage of metapopulation models is their flexibility in incorporating additional ecological processes (Gotelli, 1991). The Levins model (Eqn (1)) may be modified to include mass effect caused by the processes of source–sink dynamics (propagule rain) and the rescue effect (Gotelli, 1991). Propagule rain was previously conceptualized to account for the arrival of propagules in local communities (sink or nonsink communities) from a mainland or a very large population source (MacArthur and Wilson, 1967). This rain has the effect of making the production of propagules by the metapopulation of little consequence for colonization rates (Gotelli, 1991). In addition, the rescue effect involves a reduction in extinction probability because of the immigration of individuals from other patches, which reduces extinction rates as the landscape becomes occupied. The Levins model modified to incorporate these two components of mass effect is expressed as (Gotelli, 1991):

$$dP/dt = i(1 - P) - ep(1 - P) \quad (5)$$

A metapopulation dynamic incorporating the rescue effect and the propagule rain will have an equilibrium landscape occupancy of  $P^* = i/e$ . For the same extinction and colonization rates, this equilibrium is much larger than

that expected without the mass effect. Furthermore, species can persist even when the extinction rate is greater than the colonization rate; when immigration is greater than extinction, species tend to occupy most of the space available (Gotelli, 1991). As a consequence, the mass effect represents a strong force promoting species viability in local communities, raising local richness, and reducing beta diversity because the species are able to persist in more communities (Holyoak et al., 2005b). Immigration to local communities is determined by the influx of individuals from the metacommunity. Thus, the larger the centrality (i.e., lower the isolation) of a local community becomes, the greater the importance of immigration and the mass effect (Figure 3). When considering a single species pool, the probability of patch occupancy may be translated into an expected richness by multiplying this probability by the number of species in the pool (Hanski, 1999, 2010). The expected pattern is a poor representation of species across isolated communities—that is, a nonlinear increase in species richness with all species of the pool present among more central communities (Figure 3). This result is congruent with predictions of nonneutral models considering species-specific demographic parameters (Loreau, 2010; Loreau and Mouquet, 1999). The metacommunity may be considered as comprising two pools of species, one with attributes that promote better performance in central communities and the other with attributes that promote better performance in isolated communities (e.g., Chase and Shulman, 2009; Welsh and Hodgson, 2011). Both groups of species have inverse relationships in colonization and/or extinction rates across an isolation gradient. In the framework of a Levins metapopulation model for each pool and, for simplicity, considering only trends in colonization rates, the combination of species from the two pools at intermediate levels of isolation contribute to a humped pattern of diversity (Figure 2(b) and Arim et al., 2002). When we consider species interactions for the dominant/subordinate species



**FIGURE 3** Expected trend in richness across an isolation gradient under the influence of *mass effect*. The metapopulation model incorporating the rescue effect and propagule rain captures the mass effect and has a fraction of occupied patches at an equilibrium of  $P = i/e$ . The rise in immigration with increasing centrality ensures that the expected richness quickly rises to the total number of species in the pool (20 species).

discussed previously, we see that each species in the metapopulation model represents a species pool, and that total richness is determined by the sum of expected richness from each pool. When isolation has a similar effect on dominant and subordinate species, subordinate species would need better colonization capabilities in order to coexist (see [Figure 2\(a\)](#)). At the meta-community level, this may involve a transition across the isolation gradient, with subordinate species in isolated patches and dominant species in more central patches ([Figure 2\(a\)](#)). This transition would be more pronounced (even producing a U-shaped trend in species richness) when subordinate species are better colonizers in isolated patches and the dominant species better colonizers in central patches ([Figure 2\(c\)](#)).

Two main messages emerge from these metacommunity models. First, a wide range of richness–isolation patterns may be expected even from the simplest considerations of mass effect and patch dynamics mechanisms. These patterns include monotonic, humped, and U-shaped trends. Second, trait-mediated species responses to isolation and biotic interactions determine expected patterns. The operation of this second mechanism is reinforced by “species sorting,” the next metacommunity process for consideration below.

## Species Sorting

At one extreme, neutral theories (considered in the next section) predict expected patterns when ecological processes operate among individuals or species independently of their traits ([Hubbell, 2001](#); [Rosindell et al., 2011](#)). The *species sorting* view of metacommunity processes presents the other extreme ([Holyoak et al., 2005b](#)). The basic premise of species sorting is that the combination of attributes carried by a species determines its colonization and growth success in local communities ([Leibold et al., 2004](#); [Mouquet and Loreau, 2003](#)). Trade-offs in species performances under different conditions are at the heart of species sorting and most explanations of species coexistence ([Kneitel and Chase, 2004](#)). Immigration to local communities should ensure recruitment of those species with attributes well fitted to the environment of the regional pool, but immigration rates should not be so high that they produce a significant mass effect that erases trait–environment associations ([Leibold et al., 2004](#)).

[Loreau and Mouquet \(1999\)](#) introduced a metacommunity model with the potential to incorporate species sorting and mass effect, considering both as local and regional dynamics, and a dispersal parameter determining the fraction of locally produced individuals that migrate to a regional pool. In summary, this is a model that considers key components of metacommunity theory. Local communities are represented by a Levins’s metapopulation model ([Tilman, 1994](#)) in which parameters change among and within the same species across communities. Each species has local reproductive and mortality rates. As different local communities have different conditions, different species in each community will have the largest reproductive potential.

Consequently, in the absence of dispersal, each community is inhabited by a single species with the best environment–trait linkage, and regional coexistence depends on interpatch heterogeneity (Mouquet and Loreau, 2002). An intuitive and formal result of this model is that the number of species that can coexist at the metacommunity level is equal to the number of local communities (Mouquet and Loreau, 2002). In this context, species sorting determines a large variation of trait performance among communities, with a hypothetical extreme of single local communities selecting for unique combinations of species traits. A further outcome that emerges from this concept is the possibility of local coexistence when the reproductive rates of different species are different in local communities but similar across the whole metacommunity (Mouquet and Loreau, 2002).

When there is a gradient of dispersal rates, such as the continuum that may exist across the space between isolated and central communities, species sorting is predicted to function as a strong structuring mechanism at low dispersal rates, progressively weakening when higher dispersal rates enhance local abundance of the best competitors at the metacommunity level—for example, by mass effect. Mouquet and Loreau (2003) validated this prediction by showing that local diversity ( $\alpha$ ) tracks a humped trend with dispersal, while beta diversity ( $\beta$ ) and gamma diversity ( $\gamma$ ) decay with dispersal rate (Mouquet and Loreau, 2003). The analysis of local food webs connected by dispersal suggests that food web branching also tracks a humped association with dispersal rate, corroborating the humped association between local richness and dispersal (Pillai et al., 2012). However, the inclusion of stochasticity into dispersal rate eliminates this association, moving the richness mode to higher dispersal rates (Matias et al., 2013). The humped trend may be reinforced when keystone predators enhance local coexistence or weaken when predation or competition promotes species extinction (Kneitel and Miller, 2003).

## Neutral Mechanisms

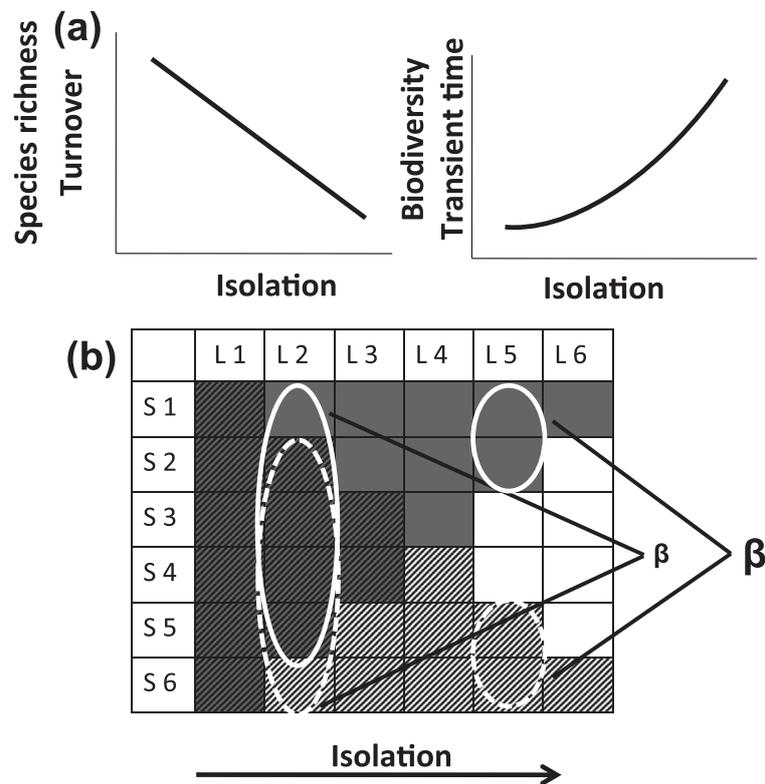
Neutral theories are based on the assumption that organismal traits have no selective role. Thus, whatever the variation in phenotypic attributes observed among species or individuals, all have equal chances of survival and reproduction (Hubbell, 2001). Neutral theories may incorporate processes of competition (Hubbell, 2001), disturbance (Kadmon and Benjamini, 2006), landscape structure (Borthagaray et al., 2014b; Economo and Keitt, 2008), or any sound ecological/evolutionary mechanism. It is not the simplicity or complexity of a theory that determines its neutral status, but rather the fact that organism and/or species traits have no role in the operation of these processes.

The island biogeography model of MacArthur and Wilson (MW) (1967) assumes a species pool on a mainland that serves as a source for island colonization. It further assumes that colonization and extinction rates are determined by island isolation and area, but for each island these rates are

equal among all species (MacArthur and Levins, 1967; MacArthur and Wilson, 1967). As a consequence, the MW model represents a neutral theory at the species level (Hubbell, 2001). The expected species richness on an island is a result of the colonization–extinction balance, which determines a dynamic equilibrium whereby the number of species on the island remains fixed, but the composition changes at a constant rate (Gotelli, 2008; MacArthur and Levins, 1967). The model considers both local (area) and landscape (isolation) determinants of local community richness and species turnover. Two main predictions on isolation emerge from this model: (1) species richness decreases with isolation, and (2) species turnover also decreases with isolation. As a consequence of these two predictions, a third may be proposed: (3) as a result of the sampling effect, beta diversity between communities that are similarly isolated increases at higher isolation levels. When there is a progressive colonization process with immigrant species coming not only from the mainland but also from other islands, a nested pattern can emerge at the metacommunity scale. Across a gradient of community isolation, poorer communities tend to be subsamples of richer ones (Patterson and Atmar, 1986).

Throughout the 10 years following the publication of *The Unified Neutral Theory of Biodiversity and Biogeography* (Hubbell, 2001), responses to the concept changed from virulent attacks to acceptance of neutral processes as main components of ecological theory (Holyoak et al., 2005b; Rosindell et al., 2011). However, debate about the role of neutral processes and the approach to neutrality in Hubbell’s formulation remains ongoing (Clark, 2012; Clarke and Johnston, 1999; Shipley, 2010b). The focus of Hubbell’s theory on the analysis of ecological processes (with an underlying premise of neutrality at the individual level) confirmed previous predictions and significantly expanded the range of ecological patterns and processes for consideration (Rosindell et al., 2011). The accurate prediction of the species abundance distribution (SAD) by neutral models was previously considered a validation of the theory. However, it became evident that the same SAD pattern may be expected under the operation of neutral, quasi-neutral, or nonneutral mechanisms (Mouquet and Loreau, 2003; Rosindell et al., 2011). Consequently, the reproduction of SAD patterns may actually be considered a necessary but insufficient condition for the validation of alternative ecological mechanisms. Simultaneous focus on SAD and other patterns, such as species–area relationships and temporal or spatial turnover, is considered a more appropriate approach to the analysis of neutral theories (Rosindell et al., 2011). Major predictions of neutral models, including MacArthur and Wilson’s, are summarized in Figure 4.

Neutral and niche theories may be considered two ends of a conceptual continuum rather than contrasted alternatives (Gravel et al., 2006; Shipley, 2010a). When the immigration rate is sufficiently high that it surpasses the signal of local community selection for organismal traits, a neutrality domain emerges (Ai et al., 2013). Under these circumstances, it may be predicted that more central communities will be influenced by a mass effect than those that



**FIGURE 4** Main predictions of neutral models on the effect of isolation on community structure. (a) Isolation is expected to reduce species richness and slow temporal turnover (left panel). Beta diversity among isolated communities is expected to increase with isolation and transient time to community attractors (right panel). (b) At the metacommunity level, a nested pattern is expected to emerge when immigrants to isolated communities come from closer and less-isolated communities. More-isolated communities contain a subset of species compositions of those nearer to the species pool. Two possible nested patterns (white with cross-hatching as well as gray) are depicted in a species (S) × localities (L) matrix. Black and crosshatched cells indicate the presence of species S in locality L, whereas white cells indicate absences. Two of any of the communities (encircled by white dashed or continuous lines) are more likely to share species (low beta diversity) when they are in more-central locations.

are isolated, which reduces the role of traits on community assembly and enhances neutral dynamics. Thus, for neutral dynamics to operate in some local communities, niche-mediated species assemblage should be operating at the metacommunity level.

Significant improvements have been made in the estimation of neutral model parameters from field data (Munoz and Couteron, 2011; Rosindell et al., 2011). Modeling and empirical parameterization of neutral dynamics should become relatively straightforward with novel approaches (Munoz and Couteron, 2011; Rosindell et al., 2011). Furthermore, as the niche–neutral continuum becomes more widely recognized, it will be necessary to develop a methodology that is able to identify systems at any point on this gradient. The analysis of community assembly through MaxEnt formalisms may well provide the appropriate procedure for making these determinations across the continuum (Shipley et al., 2006).

## Theory Data

Empirical support for the construction of ecological theory depends on clear assumptions and predictions, and testing with procedures that either support them or do not. The four paradigms of metacommunity ecology (also termed “views” or “mechanisms”) have explicit assumptions and predictions (Figure 1). However, empirical approaches using field data (Cottenie, 2005), and even experimental analyses (Logue et al., 2011), are limited in their ability to provide adequate information to make choices among mechanisms. The isolation of a single paradigm operating independently of the others may be impossible in many cases. While this complexity is part of the natural world, it is nevertheless rewarding to seek approaches that would disentangle the paradigms. In this context, we promote the view that further application of graph theory for the estimation of proxies of local and regional dispersal (Altermatt, 2013; Economo and Keitt, 2010), and the incorporation of MaxEnt analysis of functional diversity (Shipley et al., 2006) will likely markedly enlarge the metacommunity ecologist’s toolbox and contribute to the construction of robust theory.

Several methods are currently used to explore metacommunity mechanisms through the analysis of field data. Spatial autocorrelation in community structure has been used as a proxy of dispersal, whereby the scale of correlation is assumed to be proportional to dispersal (Shurin et al., 2009; Soininen et al., 2007). Partitioning of variance dissects the total variation in a community matrix into unique environmental and spatial components, and is capable of separating each of these components independently of one or all of the others using a purely statistical procedure (Cottenie, 2005). It is usually assumed that environmental components represent local filters, that spatial components represent dispersal limitation, and that their interaction term is difficult to interpret (Meynard et al., 2013). Another approach involves the analysis of a species site-by-species incidence matrix (Meynard et al., 2013) that detects structures that may support random assembly, competition, or environmental filtering. The combined use of this matrix analysis and the partitioning of variance into components that are environmental or spatial may robustly analyze empirical data for the determination of metacommunity mechanisms (see Meynard et al., 2013). Finally, neutral models and the relative deviation between observed pattern and neutral expectations are now amenable to relatively straightforward computation (Munoz and Coueron, 2011; Rosindell et al., 2011). As a consequence, the evaluation of neutral mechanisms—for example, through analysis of a spectrum of communities with different dispersal rates—may function as a powerful empirical procedure. A potential limitation of this approach is that there are several potential neutral models for consideration. Consequently, a deviation from model expectations may represent a limitation of the model considered rather than of the magnitude of the neutral mechanisms. On the other hand, the fitting procedure of some null models may involve very flexible equations that represent

a wide range of data spanning neutral and nonneutral mechanisms (McGill, 2003). MaxEnt analysis of metacommunity patterns provides an alternative measure of neutrality; it is an analysis conditioned to the set of traits observed among species, but independent of any particular neutral mechanism.

The degree of isolation of a local community is accepted as a good proxy for the potential dispersal experienced by a local community (Altermatt, 2013; Brown and Swan, 2010; Economo and Keitt, 2010). Isolation could be represented by the distance of a local community to other patches—for example, those at headwaters (Miyazono and Taylor, 2013). However, the explicit consideration of metacommunity networks makes it possible to use several alternative and complementary measures of isolation that provide quantitative and continuous estimations of centrality. In addition, the same degree of community isolation may represent a strong or a weak barrier to dispersal depending on the dispersal abilities of species (Borthagaray et al., 2012; Economo and Keitt, 2010; Keitt et al., 1997; Urban and Keitt, 2001). As a consequence, the organismal perspective has to be considered in the analysis of a metacommunity pattern. The problem of incorporating individual perspective into the definition of a metacommunity is not new, but it has seldom been evident in ecological thinking following the pioneer studies in community ecology (Holyoak et al., 2005). In the next section, we review the main network metrics that may be used to estimate the relative centrality—isolation of local communities as proxies of dispersal.

## Metacommunity Networks

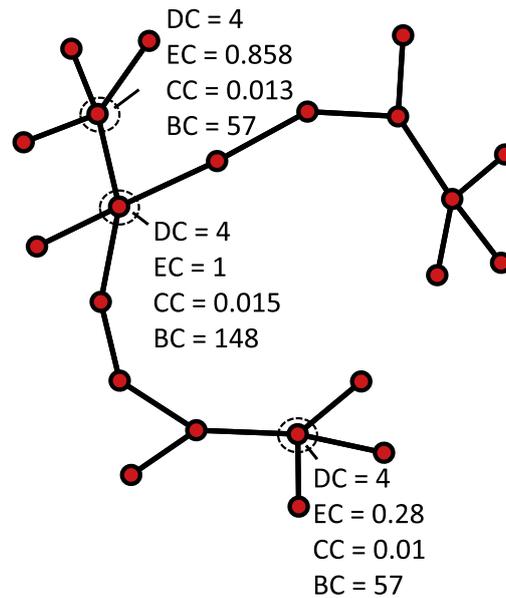
Exploring the role of the metacommunity network on communities and metacommunity structure will require comparisons of both (1) local communities with different patterns of insertion within the network and (2) different metacommunities with contrasting structures at the network level. Graph theory provides an exceptional procedure for progress on these two issues (Urban and Keitt, 2001). Graph theory has long been used as a framework for analysis of ecological networks considered as food webs (Cohen et al., 1990; Pimm, 1982), of mutualistic networks (Bascompte et al., 2003), and increasingly in landscape ecology (Keitt et al., 1997; Urban and Keitt, 2001). The central role of graph theory in advancing a spatially explicit approach to metacommunity ecology has been increasingly emphasized in recent works (Altermatt, 2013; Borthagaray et al., 2012, 2014b; Carrara et al., 2012; Economo and Keitt, 2010; Peterson et al., 2013). Graph theory provides a wide set of tools for representing metacommunities and quantifying their structures at the level of the whole network and at the level of individual communities. A metacommunity can be described by a graph defined as a set of nodes connected by links. Typically, nodes correspond to communities, and connections refer to some kind of structural or functional relationship among them—for example, the flow of individuals (Urban and Keitt, 2001). Here, we review network

metrics used to estimate the isolation (centrality) of local communities and to provide main descriptions of whole network properties. However, to determine these properties, there must be a metacommunity network, which in most cases is not easy to estimate. Thus, we will finish this chapter by describing several methodologies for empirically estimating metacommunity networks.

### *Community-Level Properties*

In recent years, centrality metrics have been used as main measures of community isolation (Ai et al., 2013; Altermatt, 2013; Altermatt et al., 2013; Borthagaray et al., 2012; Carrara et al., 2012; Desjardins-Proulx and Gravel, 2012; Economo and Keitt, 2010; Urban et al., 2009). The centrality index potentially reflects individual flows through local communities and then onward through the whole metacommunity. The various centrality metrics focus on different concepts and definitions of centrality in a network (Newman, 2010). Importantly, alternative centrality measures complement one another in the representation of different components of community isolation (see below). This becomes evident upon realization that different processes reflected in different metrics refer to different taxa. Following the same line of reasoning, the isolation or centrality of patches in different metacommunities may be better represented by different centrality measures. Therefore, it would be advantageous to calculate a large set of metrics to reflect community isolation in different ways; evaluating relative performances, the metrics account for the patterns of interest (Figure 5).

In a metacommunity context, the four major centrality metrics are degree, eigenvector, closeness, and betweenness (see Table 1) (Economo and Keitt, 2010; Estrada and Bodin, 2008). Larger values of centrality indicate lower levels of community isolation (Economo and Keitt, 2010). *Degree centrality* is the number of direct connections between a community and its neighbors—for example, direct links between patches (Freeman, 1979; Wasserman and Faust, 1994). The term “connectivity of a node” has also been used to refer to degree centrality. *Eigenvector centrality* ranks communities not only by the number of direct connections, but also by the number of connections that their neighbors have (Bonacich, 1972; Wasserman and Faust, 1994). In this sense, it may be seen as an extended degree centrality, since it is proportional to the sum of the degree centralities of the community neighbors. Definitions of closeness centrality and betweenness centrality are based on the length of the shortest path between communities (Freeman, 1979; Wasserman and Faust, 1994). *Closeness centrality* is the reciprocal of the average length of the shortest path between the reference community and all others; it provides a representation of how close or how far a community is from the remaining communities in the metacommunity. A main limitation of closeness is that it cannot be calculated for all communities in a disconnected metacommunity since two unconnected communities do not have a finite distance between them (Opsahl et al., 2010).



**FIGURE 5** Estimation of alternative indices of centrality (the reverse of isolation) in a hypothetical metacommunity. A circle represents local communities and lines the connections among them. The dashed circles indicate the locations of three communities for which alternative centrality indices were estimated: DC: degree centrality; EC: eigenvector centrality; CC: closeness centrality; BC: betweenness centrality. Each index emphasizes a different component of community isolation; the communities considered here have the same local connections (DC), but have different isolations measured in terms of the connections between their neighborhoods and the neighborhoods of their neighborhoods (EC), relative distance to all other communities (CC), and roles as stepping stones for individual flow across the whole community (BC).

Alternatively, closeness may also be expressed by its inverse value to represent isolation, a metric termed *farness* (Altermatt, 2013; Newman, 2010). *Betweenness centrality* describes how often a community acts as a mediator on the shortest path between two other communities, identifying key connectors—that is, stepping stones of individual flow to the rest of the metacommunity. The different centrality metrics emphasize different aspects relating to the spatial scope considered (Figure 5). Degree centrality highlights the potential flow of individuals through the local neighborhood. Eigenvector centrality expands the potential flow of individuals to a larger neighborhood. Closeness centrality is a measure of how long it takes an organism to move sequentially from one patch to all other patches in the metacommunity (Altermatt, 2013). Betweenness centrality emphasizes the bridging role of the patches in maintaining metacommunity connectivity beyond the local scale.

Other centrality metrics have been suggested to emphasize metacommunity structure at intermediate scales. Among them, the *k-neighborhood* metric is defined as the number of communities that are within a *k*-shortest path from the focal community (Economo and Keitt, 2010). *Subgraph centrality* measures the number of times a community occurs in all subgraphs or in closed loops within the metacommunity, with weighting according to their

**TABLE 1** Definition of Centrality Indices and Their Calculation with R Program

Index	Definition	R Package (Function)
Degree centrality	Number of neighboring communities	sna (degree); Igraph (degree)
Eigenvector centrality	Scores communities not only by their immediate connections but also by the degree of connection	sna (evcent); Igraph (evcent)
Closeness centrality	Calculates how close a focal community is to all other communities	sna (closeness); Igraph (closeness)
Betweenness centrality	Quantifies how frequently a community is on the shortest path between every possible pair of the other communities	sna (betweenness); Igraph (betweenness)
k-neighborhood	Number of communities within distance k of the focal community	Igraph (neighborhood.size)
Subgraph centrality	Number of closed loops in which a focal community is involved	Igraph (subgraph.centralitiy)

size (Estrada and Rodríguez-Velázquez, 2005). All these metrics may be calculated with R software (R Development Core Team, 2013) (see Table 1). Parameter estimation is based on an adjacency matrix in which each element is 1 if two communities are connected and otherwise 0 (Urban and Keitt, 2001).

A final caveat for mention is the fact that centrality indices are relative measures of local community importance. The value of each index as an indicator of the degree of community isolation depends on the spatial arrangement of the other communities within the metacommunity. In this sense, to make results comparable among metacommunities, it would be appropriate to standardize centrality metrics to the size of the metacommunity or to normalize them so that they sum to 1.

### *Metacommunity-Level Properties*

A well-supported advance in the empirical association between metacommunity structure and function is based on the comparative analysis of different metacommunities (e.g., Bertuzzo et al., 2011; Carrara et al., 2012). Although slower than the development of theoretical studies (Driscoll and Lindenmayer, 2009), empirical explorations are now underway (Burns, 2007; Driscoll and Lindenmayer, 2009). A future challenge for advances in this field will be the recording and comparison of contrasting metacommunity structures

and associated biological information. This procedure is of relevance because properties of network structure strongly affect metacommunity dynamics (Economo and Keitt, 2008; Gilarranz and Bascompte, 2012). Thus, we now present alternative metrics for the description of structural properties at the level of the whole network.

Three of the most widely used and characteristic structural properties of any kind of network are *linkage density*, *connectance*, and *diameter*. Connectance is the number of connections or links realized ( $L$ ) divided by the maximum possible number of links (Newman, 2003; Proulx et al., 2005; Williams et al., 2002). In a metacommunity with  $lc$  local communities, connectance is calculated as  $(2 \times L/lc \times (lc-1))$ . A metacommunity with a high connectance probably has more redundancy in connections among local communities, which may foster robustness when link and patch removal occur (Melián and Bascompte, 2002). At the same time, higher connectance may promote disease propagation and global extinction because of the synchronization of local dynamics (Liebhold et al., 2004). Linkage density is defined as the average number of realized links per local community and is calculated as  $(L/lc)$ , where  $(L)$  is the total number of links in the network and  $(lc)$  is the number of local communities. The diameter of a metacommunity represents the number of steps necessary for movement through the whole metacommunity. Estimations of diameter are based on the distribution of the shortest paths between all pairs of local communities. Thus, diameter has been defined as the length of the number of links in the longest path among shortest paths between all pairs of communities (Newman, 2003; Urban and Keitt, 2001; Wasserman and Faust, 1994). It is therefore necessary to determine all of the shortest paths between all pairs of communities in the network and then find the longest among them. Diameter has also been defined as the average of the shortest paths between all pairs of communities in the network (Proulx et al., 2005), and also as the characteristic path length (Williams et al., 2002). A good description of metacommunity structure may be obtained by considering linkage density, connectance, and diameter.

Other basic and widely used metrics to describe network structure are based on frequency distributions rather than on single parameters. For example, linkage density estimates the mean degree, which in several networks provides a good description of the connection between local patches. However, when the distribution of links per patch is markedly asymmetric—that is, most patches with few links and a few with several connections—a focus on whole distributions may be a more appropriate approach. *Degree distribution* (also called *connectivity distribution*) provides such a focus; it describes the frequency distribution of the number of links to each local community (May, 2006; Proulx et al., 2005). A first approach to estimating degree distribution is the construction of a histogram of community degree plotted on a logarithmic scale (see Newman, 2003). However, a better representation is obtained by using the inverse cumulative distribution, which indicates the fraction of communities

that have a degree of  $k$  or higher (Newman, 2005). The shape of this distribution represents a description of the level of heterogeneity of the whole metacommunity and is associated with the robustness of the network in maintaining the flow of individuals when increasing numbers of communities or paths are deleted (Burns, 2007; Gilarranz and Bascompte, 2012; Melián and Bascompte, 2002). The relevance of such a structure is that it represents recolonization capability from highly connected patches (Gilarranz and Bascompte, 2012). However, this would be advantageous only for individuals with long-range dispersal ability or individuals with high rates of extinction. In other cases, a homogeneous structure may be better for maintaining population persistence (Gilarranz and Bascompte, 2012).

A topological metric that complements degree distribution in the description of metacommunity structure is *degree correlation* (Krapivsky and Redner, 2001). In a metacommunity, degree correlation (also called *connectivity correlation*) is the relationship between the number of neighbors in a community and the average connections of neighbors (Maslov and Snepen, 2002; Melián and Bascompte, 2002). The slope of this correlation indicates the level of spatial aggregation of the overall network. Links between highly connected communities generate a cohesive structure, but when such links are suppressed, a compartmentalized metacommunity structure would be expected (Melián and Bascompte, 2002).

The properties described above emphasize large-scale structures that affect the dispersal and interchange of organisms through the whole metacommunity. *Modularity* is a property of intermediate scales between local community and metacommunity levels; it is defined as the degree to which some groups of communities have a higher probability of mutual flows of organisms as opposed to flows to other communities (May, 1972; Newman and Girvan, 2004). In this sense, modularity detects groups of communities (called modules or compartments) with relatively high numbers of mutual connections favoring the movement of neighboring individuals, even when each individual is able to reach any community in the landscape (Borthagaray et al., 2014b). Although modularity was proposed as an early key metric of networks (May, 1972), the intermediate level of structure captured by modularity has rarely been considered (Borthagaray et al., 2014b). It should be noted that other metrics have been developed to identify modules and compartments (see Bodin and Norberg, 2007; Urban and Keitt, 2001), but only after the recent development of robust modularity-detecting algorithms (Guimerà and Amaral, 2005; Newman and Girvan, 2004) have modules and compartments been widely detected in ecological networks (e.g., Olesen et al., 2007; Stouffer and Bascompte, 2011).

### *Weighted Metacommunity Networks*

To this point, all metacommunity- and community-level properties have been defined for an unweighted and undirected network and calculated from an

adjacency matrix (a 0–1 matrix indicating the presence or absence of individual flows between all pairs of communities). Alternatively, distance or dispersal matrices are used to define weighted connections between local communities. A *distance matrix* is one in which each element corresponds to a distance between local communities. This distance is measured as the minimum edge-to-edge or centroid-to-centroid Euclidean distance (Urban and Keitt, 2001). In addition, the distance between patches may be a biological distance (e.g., the Jaccard index). Another alternative is the *dispersal matrix* in which each element is defined as the probability that an individual in a community moves to another community. Dispersal probability is often approximated by a negative exponential function of the distance between two communities (Bunn et al., 2000; Hanski, 1999; Urban and Keitt, 2001), but other distributions may also be used (Clark et al., 1999). Therefore, community-centrality metrics and metacommunity metrics for weighted networks are based on the sum of the link weights rather than on the number of links (e.g., Estrada and Bodin, 2008); that is, a distance is defined as the sum of the link weights instead of the number of links between two communities. For example, the length of the shortest path between communities that defines closeness centrality, betweenness centrality, or the diameter of a metacommunity is calculated by summing the link weights. Finally, community-centrality metrics may also be defined by combining both the number of communities to which a focal community is connected and the sum of link weights (Opsahl et al., 2010).

Importantly, an adjacency matrix may be generated from the distance matrix or the dispersal matrix defining a threshold distance or probability to determine a link between two communities (Bunn et al., 2000). Two communities in a network are connected by a link when the separation between them is below the threshold distance (Keitt et al., 1997; Urban and Keitt, 2001).

Moreover, metacommunity network structure may be asymmetric, implying a directed network (e.g., a river). Thus, the distance defining the connection from community  $i$  to community  $j$  is different from the reverse path from community  $i$  to community  $j$ . Accordingly, two types of degree centrality are differentiated. In-degree, defined as the number of links that end in community  $i$ , and out-degree defined as the number of links originating in community  $i$ . Similarly, two types of closeness and betweenness centrality may be estimated for a directed network. These metrics may be calculated with the functions specified in Table 1 and executed with R software (first indicating that the matrix is directed and weighted) (R Development Core Team, 2013).

Patch isolation and its effect on immigration rate have been extensively considered by practitioners of metapopulation ecology (Hanski, 1999). An interesting approach is the estimation of the potential immigration rate (formerly termed connectivity,  $S_i$ ) to a local community from all other communities, taking into consideration their distances, areas, occupancy

probabilities, and a kernel function of decay in dispersal with distance to the source (Hanski, 2010). With this approach, the colonization rate of a focal patch is defined as the sum of the contributions from all possible source patches. These contributions are weighted by three factors: (1) the areas of the source  $A_j$  and focal patches  $A_i$ , (2) the distance from the focal patch to the source patch  $d_{ij}$ , and (3) the probability of the source patch being occupied  $p_j$ . In addition, the effect of areas on individual flows may be elevated to an exponent to account for nonlinear effects ( $A_i^{\epsilon_{im}}$  and  $A_j^{\epsilon_{em}}$ ), and the distance effect may be an exponential (with an  $\alpha$  decay parameter) or any appropriate function (Hanski, 2010):

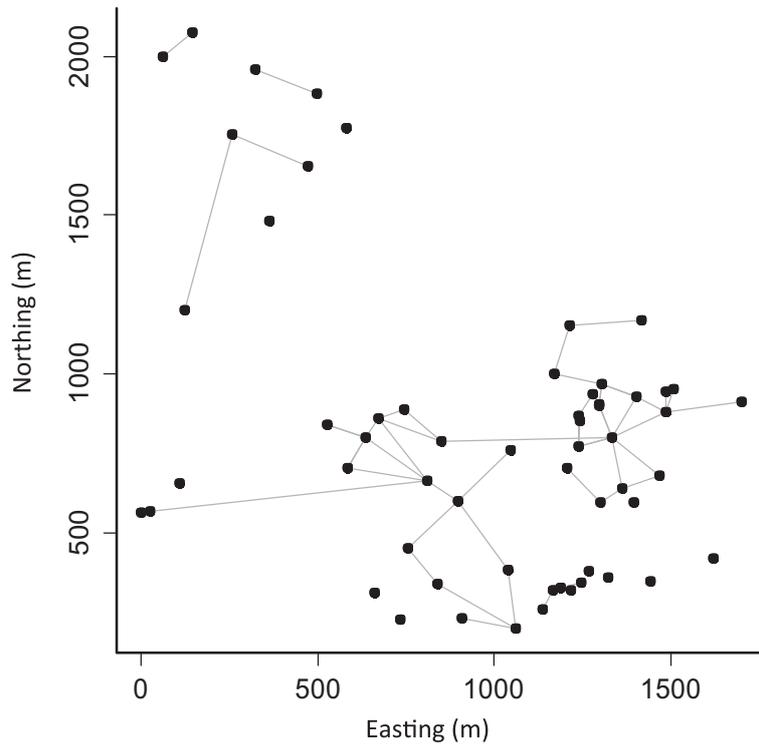
$$S_i = A_i^{\epsilon_{im}} \sum A_j^{\epsilon_{em}} p_j \exp(-\alpha d_{ij}) \quad (6)$$

In estimating local community immigration rate, potential immigration from each of the other communities is considered. Combined vectors of immigration rates for all patches can be used to estimate a migration matrix and the associated migration-weighted graph. Finally, it should be emphasized that the parameter of this metric of centrality and the immigration rate may be directly estimated from the occurrence pattern, making this procedure a powerful tool for empirical approaches (Hanski, 2010).

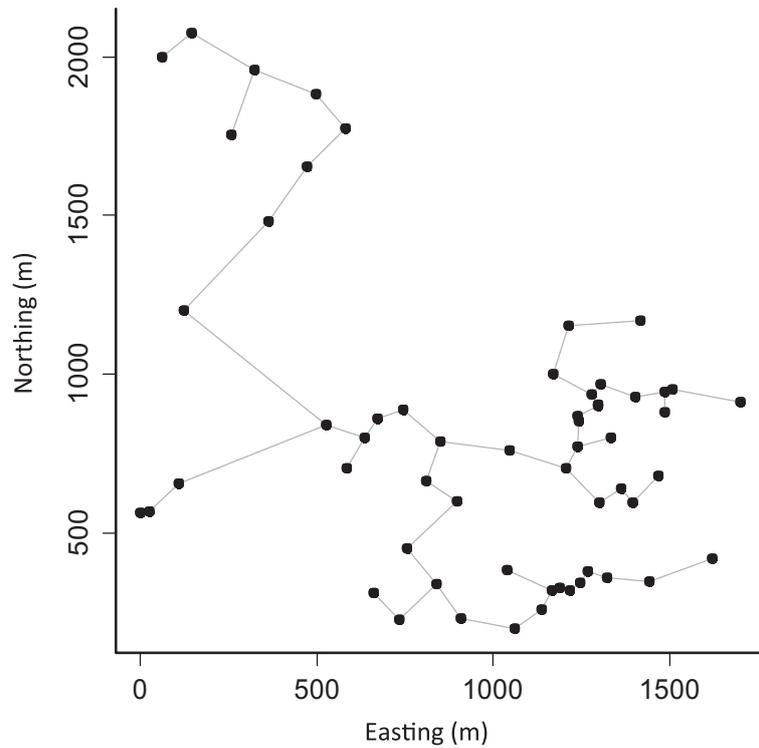
### *Methodologies for Estimating Metacommunity Networks*

A main challenge in the analysis of metacommunities is identification of network configuration (Jacobson and Peres-Neto, 2010)—that is, the spatial arrangement of communities and their connections, through which individuals move. In this sense, a natural network configuration is one defined for organisms subjected to directional dispersal driven by wind and water flows (Figure 6, Altermatt, 2013; Vanschoenwinkel et al., 2008a,b). Similarly, using molecular or genetic approaches it is possible to establish the connectivity pattern between communities and determine the metacommunity structure (Becker et al., 2007; Fortuna et al., 2009).

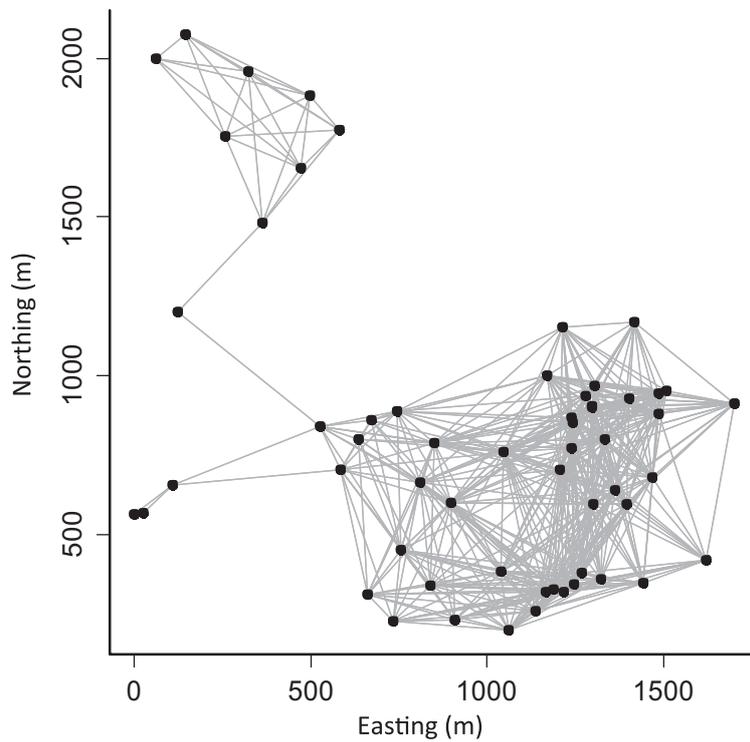
However, in most cases the metacommunity configuration is unknown or the level of sampling effort required for its determination cannot be achieved. Two readily applicable approximations for estimating spatial networks are the minimum spanning tree (MST) and the percolation network (Figures 7 and 8). Both methodologies define fully connected networks but differ in the criteria for connecting two communities. The MST connects every local community with the shortest path length—that is, with the minimum number of links to ensure that all patches are connected to a single graph. The MST represents the backbone of the network maximizing the flow of individuals with different dispersal abilities among communities (Urban and Keitt, 2001; Urban et al., 2008). Notice that in this approximation only the number of links (not their lengths) defines the network structure. The percolation network is defined as a graph in which patches are



**FIGURE 6** A potential metacommunity network for a system of temporary ponds located in Uruguay ( $34^{\circ}25'47''S$ ,  $53^{\circ}98'10''W$ ). The ponds (nodes) are sporadically linked by water corridors (lines) as the system drains after heavy rainfall events. The physical connection between communities is an intuitive approach to estimating the metacommunity network. However, the functional metacommunity network may be different.



**FIGURE 7** Minimum spanning tree (MST) for the temporary pond system in [Figure 6](#). An MST is the shortest network that includes all the nodes in the graph ([Urban and Keitt, 2001](#)).



**FIGURE 8** Percolation network for the temporary pond system in [Figure 6](#). This network is obtained by linking the pairs of nodes that reach the minimum distance linking the whole patch system and form a single cluster. In this case, the percolation threshold is 539 m.

connected when the distance between them is less than a threshold distance, which is the minimum distance (i.e., the percolation point) at which all patches are connected in a single network ([Rozenfeld et al., 2008](#); [Urban and Keitt, 2001](#)). The structure of this network with a threshold behavior is reminiscent of other landscape connectivity metrics such as connectedness or diameter ([Keitt et al., 1997](#); [With and Crist, 1995](#); [Keitt et al., 1997](#)). Similarly, the ability of organisms to disperse among communities typically fits a pattern of abrupt transitions from movements on local scales to movements that allow potential access to all parts of the landscape beyond the critical threshold distance ([Borthagaray et al., 2012](#)).

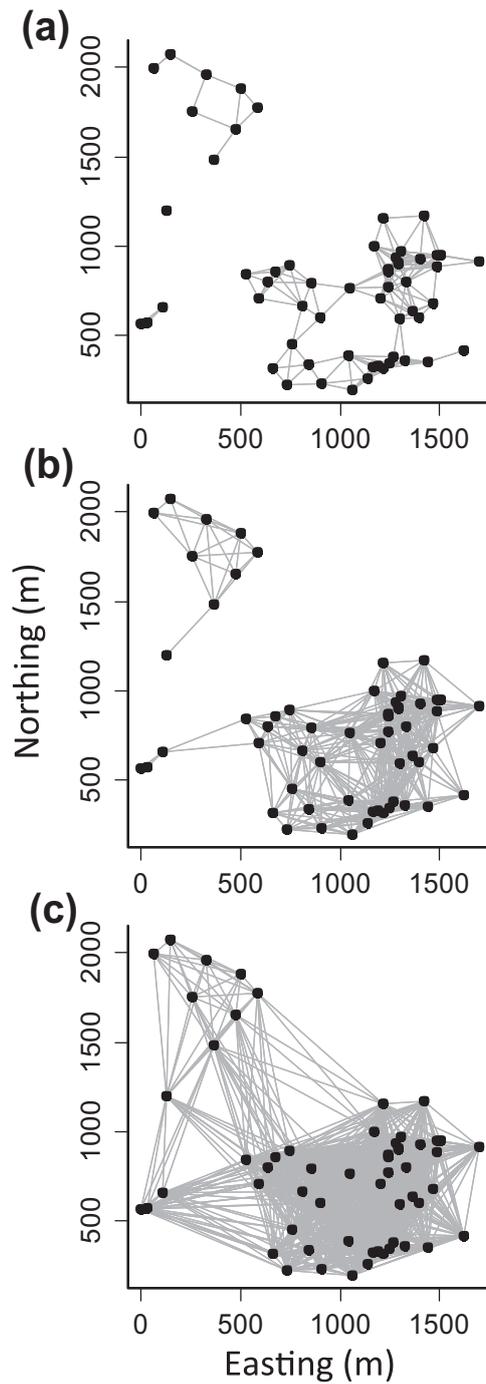
Although the MST and percolation network provide robust estimations of metacommunity networks, they may differ significantly from the landscape perceived by the organisms under consideration, or poorly represent the processes shaping local community structure. Local communities harbor species with a wide range of biological attributes that likely determine the spatial scales at which they experience the landscape ([Borthagaray et al., 2012, 2014b](#); [Keitt et al., 1997](#)). Moreover, the same geographic distance between a pair of communities may be perceived as either a weak or a strong barrier to dispersal by different organisms that are part of the same metacommunity. Under these circumstances, exploration of a wide set of networks defined by a gradient of threshold distances provides an alternative approach

to determining metacommunity networks (e.g., [Borthagaray et al., 2014b](#); [Urban and Keitt, 2001](#)). This gradient is the continuum of geographic distances from the minimum to the maximum edge-to-edge Euclidean distance between two communities, which reflects the wide range of potential dispersal distances in a metacommunity pool ([Figure 9](#)). As the threshold distance increases, communities are connected into larger components that are themselves connected at even greater threshold distances ([Urban and Keitt, 2001](#)). In addition, a biological distance such as the Jaccard index, or a combination of both distance indices, may be more meaningful for connecting two communities than geographic distance alone ([Figure 10](#)). Biological indices may demonstrate that geographically close communities are isolated from one another, while distant communities are connected ([Fortuna et al., 2009](#)). Another methodology uses modeling of dispersal based on individual biological attributes to determine the putative connections that define metacommunity configuration (e.g., [Moritz et al., 2013](#)). An alternative procedure, which has been well developed in metapopulation ecology, is calculation of the incidence function; this function has the potential for application in a metacommunity context ([Eqn \(6\)](#); [Melian and Bascompte, 2002](#)).

Finally, we propose a new methodology for constructing a metacommunity network based on maximization of coherence with a community attribute (e.g., diversity or productivity). This approach consists of four steps: (1) constructing a set of metacommunity networks along a gradient of linkage distances to connect two communities; (2) calculating community-centrality metrics for each network; (3) determining the association between the centrality index and the community attribute of each metacommunity network; and (4) identifying the linkage distance and the related metacommunity network using a maximum community attribute—metacommunity network association. The underlying principle is that a community attribute—community centrality association will have an extreme value at a linkage distance congruent with the distance affecting organism flow ([Borthagaray et al., 2014a](#)).

## Maximum Entropy

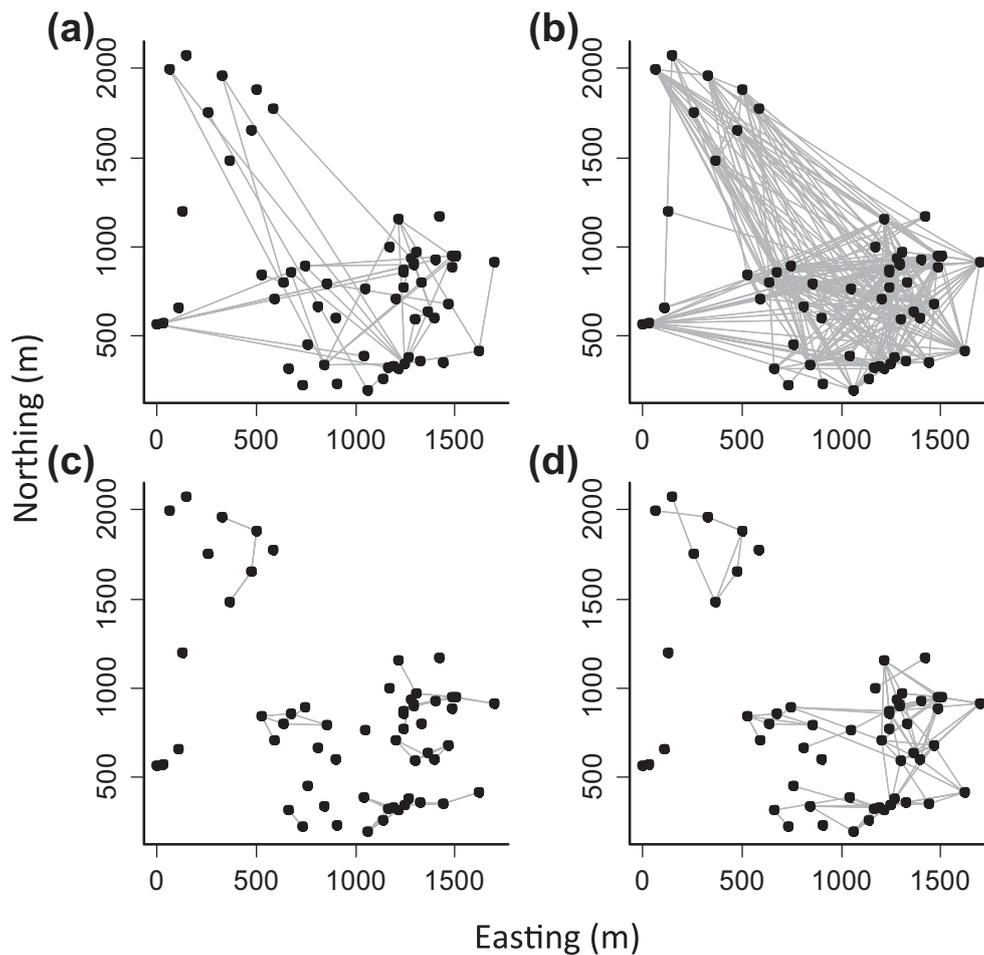
MaxEnt formalisms have performed well in niche modeling, and consequently this statistic has become a major component of the ecologist's toolbox ([Phillips et al., 2006](#)). Bill Shipley and coauthors recently proposed a novel use of MaxEnt for exploring organism trait—environment connections ([Shipley, 2010a,b](#); [Shipley et al., 2006](#)). Unraveling of this connection permits detection of major processes in community assembly that may be used to predict community structure. Shipley has provided a short, succinct review of the MaxEnt theory ([Shipley, 2010a](#)) and has also published more extensive considerations of the topic ([Shipley, 2010b](#)). As a truly groundbreaking concept, this theory is subject to extensive debate ([McGill, 2006](#); [Petchey, 2010](#)), but its good performance ([Shipley et al., 2011](#)) and demystification through the use of



**FIGURE 9** Networks obtained by three link distances: 250 m (a), 500 m (b), and 1000 m (c). All patches closer than the link distance are connected. By considering a wide range of link distances, a range of network perceptions determined by the range of dispersal abilities within the species pool may be inferred.

clear presentations (Shiple, 2010b) is consolidating its place in mainstream ecological theory.

MaxEnt translates the concept of community assembly by trait-based habitat filtering into a mathematical formalization that estimates trait roles



**FIGURE 10** Networks obtained linking the set of ponds in Figures 6–9 based on ecological distances between vegetation of local communities. The distances were estimated as Jaccard indices for pairs of ponds. The networks were obtained by linking pairs of ponds in the whole system with index values up to 0.3 (a) and 0.4 (b), and by combinations of indices up to 0.4 and spatial distances up to 250 (c) and 500 m (d).

in observed local abundances. The underpinning logic is that each trait carried by a species (e.g., body size, dispersal mode, diet) has the potential to determine outcomes of interactions with other species and with the physical environment (Keddy, 1992; Weiher and Keddy, 1999). A first examination of MaxEnt indicates that the concept brings radical change to the methodological approach for analyzing community patterns. The objective of MaxEnt is to predict the relative abundance of a species in a local community from its combination of traits. If all individuals from a local community are pooled, an average value can be estimated for each trait (e.g., mean mass, mean proportion of aerial dispersers). In MaxEnt, these measures of community-aggregated traits are termed “empirical macroscopic constraints.” An additional constraint is that relative abundances should sum to one. For any proposed combination of species abundances to conform to the local community, the values of these empirical constraints would have to be preserved.

However, consideration of the set of traits in each species identifies several combinations of species abundances that satisfy macroscopic constraints. Which of these combinations is more congruent with our knowledge of the system is as yet unknown; this knowledge gap is retained in the MaxEnt formalism, which at the same time allows selection of a particular combination of expected abundances. The selected combination is the one that maximizes entropy. Ecologists are familiar with the entropy concept in their common use of the Shannon diversity measure:  $H = -\sum p_i \log(p_i)$ . MaxEnt focuses on maximization of a related measure termed relative entropy (Shiple, 2010b):

$$\max \left( H = - \sum p_i \log \left( \frac{p_i}{q_i} \right) \right) \quad (7)$$

where  $p_i$  is the predicted abundance of species  $i$  in a local community and  $q_i$  is a prior expected abundance. This prior distribution of abundances is an additional element in MaxEnt analysis. We may have no information on the distribution of abundance among species and assume accordingly that each species has the same prior relative abundance; for example, there is a uniform prior distribution. In addition, in the absence of processes shaping local community abundances, the community should be a random sample of the metacommunity (Borthagaray et al., 2012); the relative abundance in the metacommunity is then used as the prior distribution. If the predicted distribution of relative abundances is the same as the prior distribution of relative abundances, the relative entropy is zero: there is no increase in our knowledge of the system. On the other hand, the larger the discrepancy between  $p_i$  and  $q_i$  the more our knowledge increases. MaxEnt maximizes this increase in knowledge but is restricted to macroscopic constraints. The pressing issue now is application of a method for assigning a relative abundance  $p_i$  to each species in agreement with macroscopic constraints and maximizing relative entropy. “Lagrange multipliers” perform this function (Shiple, 2010a), for which there is a general solution, the “Gibbs distribution”:

$$p_i = \frac{q_i \cdot \sum_{j=1}^K X_{ij} \cdot \lambda_j}{\sum_i q_i \cdot e^{-\sum_{j=1}^K X_{ij} \cdot \lambda_j}} \quad (8)$$

This ungainly formula is a powerful tool for use in functional and meta-community ecology. The parameter  $K$  is the number of traits observed in a species (e.g., mass, diet, defenses, fecundity). If no trait were measured, the expected relative abundance would be the prior relative abundance  $q_i$ . Parameter  $X_{ij}$  is an observation of trait  $j$  in species  $i$ , and  $\lambda_j$  is one of the Lagrange multipliers estimated by an iterative procedure (Shiple, 2010b). If observed traits have no role in species relative abundances, Lagrange multipliers will be zero and expected abundance will equal prior abundance. This is valuable ecological information, because as Lagrange multipliers become closer to zero,

the closer to neutrality will be the community assembly in relation to the traits under consideration. Parameter  $\lambda_j$  represents an estimation of the selective advantage of a species with trait  $j$  in a local community. In summary, MaxEnt focuses on functional ecology and provides a method for estimating environment–trait connections that determine local abundances of species and community structure. Notably, each metacommunity paradigm may be transformed to an explicit prediction about the values of Lagrange multipliers and expected trends across the community centrality–isolation gradient.

In the *species sorting* (SS) paradigm, different communities have different environments, and different species have different combinations of traits. To support an SS concept of community assembly, the Lagrange multipliers should change among communities, with a negative correlation between the Lagrange and community attributes. This negative association determines the differential success of species with different traits among different environments. The *mass effect* involves the movement of individuals from source to sink communities. This implies that some communities have larger Lagrange multipliers (sources) than others (sinks). *Patch dynamics* is supported by the species trade-off between colonization and competition attributes. In order to identify this mechanism, those traits with a negative correlation among species attributes (trade-off) should also have large Lagrange multipliers. This is because there is a patch dynamic requirement that those traits that negatively covary among species have effects on organism performance. Finally, *neutral dynamics* predict no association between the successes of organisms and their traits. This prediction directly transforms to a Lagrange multiplier having a value of zero. Neutrality here is always conditional on the set of attributes under consideration (Shiple, 2010b). Trends in the operational strengths of these mechanisms across a gradient of community centrality–isolation will probably predict the expected trend in Lagrange multipliers. Increases in neutrality and mass effect toward central communities on the gradient (Ai et al., 2013; Brown and Swan, 2010) should be reflected in a negative association between Lagrange multipliers and centrality. However, the increase in patch dynamics toward isolated or central communities should be reflected in a positive trend in the Lagrange multipliers involved in species trade-offs. The increase in species sorting among isolated communities (Brown and Swan, 2010) should be reflected in a larger negative association between Lagrange multipliers in isolated communities than in central communities.

Our considerations to this point emphasize the wide range of diversity–isolation relationships that may be expected and the congruence of different mechanisms supporting any single pattern. MaxEnt may be further used to disentangle alternative mechanisms beyond a single pattern—for example, if a humped trend in richness across a community isolation gradient were to originate from the mixing of two species pools, one adapted to central locations on the gradient and other adapted to isolated locations (Arim et al.,

2002), MaxEnt should identify two groups of Lagrange multipliers: one increasing, and the other decreasing with community isolation. If the humped pattern originates through species sorting in isolated communities and mass effect among central communities (Mouquet and Loreau, 2003), all Lagrange multipliers should approach zero among central communities. In general, we emphasize that the incorporation of MaxEnt analysis into community structure considerations will represent a significant advance in the testing of metacommunity theory from observational data. This is likely the most powerful approach available for advancing empirical evaluations of metacommunity theory (Carrara et al., 2012; Dorazio et al., 2010; Driscoll and Lindenmayer, 2009; Logue et al., 2011).

Finally, we would like to stress that the estimation of the Lagrange multipliers is straightforward. The function “maxent” of the R software package “FD” (Laliberté and Shipley, 2011) estimates Lagrange multipliers starting from the set of macroscopic values in local communities, the set of traits values, and a prior distribution of abundances. Furthermore, the MaxEnt analysis of community assembly will become even more straightforward since the recent recognition of its equivalence to Poisson regressions (Renner and Warton, 2013; Warton et al., in press). This will expand the range of trait–environment associations for consideration, incorporate statistical methods for model validation and contrasts among models, and in general incorporate all the machinery of generalized linear models.

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