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Coexistence, dispersal and spatial structure in metacommunities: a stochastic model approach

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Abstract

We propose a stochastic model for interacting species in a metacommunity in order to study the factors affecting the intensity of the competition/colonization trade-off as a coexistence mechanism in metacommunities. We particularly focus on the role of the number of local communities and the number of refuges for the inferior competitor. The stochastic component is associated with the dispersal process and is represented by Poisson random measures. Thus, this stochastic model includes two dynamic scales: a continuous one, which refers to the interactions among species, and a low frequency one, referring to dispersal following a Poisson scheme. We show the well-posedness of the model and that it is possible to study its long-term behavior using Lyapunov exponents; the extinction of a species is associated with a negative slope in the time trajectory of the dispersal rate of the inferior competitor, and that it becomes less intense as the number of local communities increases, while the opposite is true with an increase in the number of refuges for the inferior competitor. We also show that under a priority effect type of scenario, dispersal can reverse priority effects and generate coexistence. Our results emphasize the importance of coexistence mechanisms related to the topology of the system of local communities, and its relationship with dispersal, in affecting the result of competition in local communities.

Keywords Metacommunity · Island biogeography · Lotka-Volterra model · Poisson measure · Lyapunov exponent · Trade-off · Priority effect

Introduction

Coexistence and diversity in local communities connected by dispersal, or metacommunities, have been shown to be associated with the interplay between local and regional processes (e.g., Ricklefs 1987; Hanski 1982; Cornell and Lawton 1992; Holt 1993; Loreau and Mouquet 1999; Hubbell 2001). Prominent among the first are densitydependent process associated with interspecific (e.g., competition and predation) and intraspecific interactions (e.g., Allee effects, intraspecific competition) as well as the spatial and temporal variation in abiotic conditions and the matching between species life-histories and habitat templates (e.g., Southwood 1977). that the spatial structure of habitats (e.g., size and distance among patches), their temporal dynamics and their heterogeneity in quality, are important components of habitats templates that affect persistence in metapopulations (e.g., Marquet 1997; Hanski and Ovaskainen 2000; Keymer et al. 2000) and coexistence in local communities (Chesson 1994; Neuhauser and Pacala 1999; Bolker and Pacala 1999; Chesson 2000; Murrell and Law 2003) and metacommunities (e.g., Forbes and Chase 2002; Holyoak 2000; Mena-Lorca et al. 2006). These effects are mediated by the interaction between species life-histories and the spatio-temporal characteristics of their habitats and in particular by those life-history traits that affect dispersal and competitive ability, which in turn affect both colonization and extinction rates. Dispersal, in particular, is fundamental to account for coexistence and diversity in metacommunities, through a series of mechanisms such as rescue effects, sourcesink dynamics, by mechanisms intrinsic to dispersal itself (Aiken and Navarrete 2014), and by trade-offs between

Theoretical and experimental studies have demonstrated

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competitive ability and dispersal (Amarasekare et al. 2004). This latter mechanism has been repeatedly shown to foster coexistence in competitive community and metacommunity models (e.g., Levins and Culver 1971; Hastings 1980; Nee and May 1992; Tilman 1994; Durrett and Levin 1998; Amarasekare 2003; Amarasekare 2004; Calcagno et al. 2006) and also in microcosm experiments (e.g., Cadotte 2006).

It is known that spatial heterogeneity, either in species competitive ability or habitat quality, are important in fostering coexistence in metacommunities (Amarasekare et al. 2004), what it is less known, it is how the spatial structure of local communities (i.e., habitat patches in a landscape or islands in an archipelago) may affect coexistence and diversity. MacArthur and Wilson (1967) do talk about the role of island clumping in affecting species area curves and more recently experimental evidence (Forbes and Chase 2002) and neutral models (Economo and Keitt 2008; 2010) have analyzed the impact of the spatial structure or network of interacting communities on diversity patterns. These authors show that spatial structure does have an important impact on metacommunity diversity, however, little is known on the role of spatial structure in affecting the effectiveness of mechanisms that traditionally have been used to explain coexistence in metacommunities, such as the competition dispersal tradeoff. In this contribution, we propose a stochastic model to understand the role of metacommunity spatial structure on the strength with which the competition/colonization trade-off promotes coexistence.

Introducing stochasticity and dispersal in metacommunities

The competition/colonization trade-off implies large differences in dispersal and competitive abilities among species. Dispersal is quintessentially stochastic, so the first challenge we tackle is how to develop a model for species interactions that includes dispersal as a stochastic process. Stochastic models and approaches are becoming increasingly used to understand ecological dynamics, as they may provide a better representation of biological important phenomena such as evolution, extinction, coexistence and noise-induced dynamics (e.g., Richter-Dyn and Goel 1972; Chesson 1982; Dieckmann and Law 1996; Ovaskainen and Meerson 2010; Marquet et al. 2014; Boettiger 2018). They represent a natural way of studying open systems, that is, systems that are affected by fluctuations associated with interactions with other entities, as well as with the environment wherein they are immersed. Open systems are by definition partially specified or incomplete systems, whose analysis do not consider all possible variables or entities that could affect its state and dynamics; in these cases, the external fluctuation associated with the unknown or hidden variables affecting the focal system dynamics, can be represented by noise terms (Marquet et al. 2017; Rebolledo et al. 2019). Similarly, one could include a particular type of noise or stochastic process to represent the impact of a given source of stochasticity, such as demographic stochasticity (Schreiber 2017), the impact of switching conditions in habitat quality (Luo and Mao 2007), or dispersal as proposed herein.

It is a common practice to study the impact of stochasticity in species interaction using Lotka-Volterra type models where error terms in the estimation of parameters (such as growth rates or interaction coefficients) or random perturbation in their values, as a consequence of environmental or other sources of stochasticity, can be represented by a continuous white noise in the form of a standard Brownian motion (e.g., Mao et al. 2002; Mao 2007; Du and Sam 2006; Li and Mao 2009; Hening and Nguyen 2018b; Hening and Nguyen 2018a; Xiong et al. 2019) or by including a Brownian and a jump process represented by a Poisson measure that accounts for the existence of sudden and discrete events or perturbations (e.g., volcanic eruptions) (see Bao et al. 2011; Rebolledo et al. 2019). In particular, in Rebolledo et al. (2019), the Brownian is thought of as representing rapid continuous environmental fluctuations, while the Poisson measure accounts for discrete events such as dispersal. In this contribution, we model dispersal as a Poisson process to understand its role in metacommunities, or collections of communities linked by dispersal (Wilson 1992; Leibold et al. 2004) such as island archipelagos. As we exemplify below using the classical birth-death process underlying island biogeography theory (MacArthur and Wilson 1963; Wilson and MacArthur 1967), Poisson measures drive the evolution of master equations as used in the study of abundance and richness distributions (Marquet et al. 2020) so they represent a natural way to introduce stochasticity due to dispersal in spatially structured environments.

Islands are recognized as model systems for the study of ecological and evolutionary processes (e.g., Warren et al. 2015), and have inspired the development of one of the earliest and most influential stochastic model which underlies the theory of island biogeography (MacArthur and Wilson 1963; Wilson and MacArthur 1967). The generality of this model allowed for its application to spatially heterogeneous systems of interacting entities (e.g., genes individuals, species) connected by dispersal, such as in metapopulation and metacommunity models (Levins 1969; Hanski 1982; Hubbell 2001). MacArthur and Wilson's stochastic model for the number of species found on a focal island corresponds to a birth-death process whose time evolution follows the master equation:

$$\frac{dP_s(t)}{dt} = P_{s-1}(t)\lambda_{s-1} + P_{s+1}(t)\mu_{s+1} - P_s(t)[\lambda_s + \mu_s], \quad (1)$$

for s = 0, 1, ..., S, where P_s is the probability of observing s species in a focal island, S is the *pool* of species, λ_s is the birth (i.e., colonization) rate associated with the transition from s to s + 1 species and μ_s is the death (i.e., extinction) rate associated with the transition between s to s - 1 species.

Birth-death processes, such as (1), are continuous-time stochastic processes of low frequency; that is, events occur through jumps. From a trajectorial perspective, it can be shown that birth-death processes can be written as driven by Poisson measures. For example, the trajectorial representation of a process that follows (1), allow us to get explicitly the flows or the time series of the species richness process. In particular, a process $S(\cdot)$ that follows (1) is trajectorially represented by Bansaye and Méléard (2015):

$$S(t) = S(0) + \int_0^t \int_0^\infty \left(\mathbf{1}_{\{z \le \lambda(S(u-))\}} - \mathbf{1}_{\{\lambda(S(u-)) < z \le \lambda(S(u-)) + \mu(S(u-))\}} \right) N(dz, du), \quad (2)$$

where S(0) is the initial number of species and N(dz, du) is a Poisson random measure of intensity dzdu.

Using this framework it becomes feasible to model metacommunities considering stochastic dispersal among local communities. In particular, we are interested in analyzing to what extent the spatial structure of metacommunities, through its effects on the flux of migrant individuals, affects the outcome of species interaction fostering coexistence. We tackle this question by analyzing the impact of metacommunity spatial structure on species coexistence and the competition dispersal trade-off, one of the classical coexistence mechanisms in spatially structured habitats (Amarasekare 2003; Amarasekare and Nisbet 2001; Calcagno et al. 2006). Our proposal will focus on incorporating two scales as drivers of the dynamics, a continuous scale for the among species interaction, and a low frequency one for dispersal among local communities. This will give rise to a stochastic version of a general Lotka-Volterra model with dispersal, where stochasticity will come from the low frequency jumps driven by Poisson measures and representing biomass flows among local communities. The model is illustrated by numerical simulations of competition between two species. We show that coexistence can be maintained if there is a competition colonization trade-off, however, the magnitude and functional shape of this trade-off is affected by the spatial structure of the metacommunity, the intensity of the interaction among species, and by the presence of refuges for the inferior competitor.

The paper is presented as follows: in "The model" we pose the mathematical model and equations. In "Stability"

our main result about stability is proved, and in "Numerical analysis" we develop a numerical example. A discussion and some perspectives are set in "Discussion". All proofs are found in Appendix 1. In Appendix 2 we recall the basic results of a two-competing Lotka-Volterra system in a local community and in Appendix 3 we present how dispersal affects the existence of priority effects.

Methods and results

The model

Consider a metacommunity containing *J* species and *I* local communities. Let $X_{ij}(t)$ be the biomass of the species *j* living in community *i* at time $t \in \mathbb{R}_+$. We assume that each $X_{ij}(\cdot)$ follows:

$$X_{ij}(t) = X_{ij}(0) + \int_{0}^{t} f_{ij}(X_{ij}(s))ds + \sum_{j'=1}^{J} \lambda_{jj'} \int_{0}^{t} X_{ij'}(s) X_{ij}(s)ds + \sum_{i'=1}^{I} \varepsilon_{ii'} \int_{-1}^{t} \int_{-\infty}^{\infty} X_{i'j}(s-) \mathbb{1}_{\{z \le b_j\}} N_{i'j}(dz, ds),$$
(3)

 $\sum_{i'=1}^{n} \prod_{j=0}^{n} \int_{0}^{j} \int_{0}^{j}$ where $f_{ij} : \mathbb{R} \to \mathbb{R}$ is the growth function of $X_{ij}(\cdot)$, the $\lambda_{ii'}$'s are fixed parameters representing, in general terms, the interaction among species. When $\lambda_{ij'} > 0$ the biomass of species j increases in the presence of species j' either because species j' is a mutualist or a resource (e.g., prey) of j. On the other hand, when $\lambda_{jj'} < 0$ species j decreases in biomass when j' is present because it competes or is consumed by species j'; and when $\lambda_{ii'} = 0$ species j does not interact with species j'. Intraspecific interaction are included in the growth function f_{ij} , and thus $\lambda_{jj} = 0$. The $\varepsilon_{ii'}$'s are constants representing the mean proportion of the $X_{i'i}$'s moving or migrating among communities, for each species j = 1, ..., J. When $i \neq i', \varepsilon_{ii'}$ quantifies the mean proportion of $X_{i'i}$ migrating from community *i'* towards community *i* (and then $0 \le \varepsilon_{ii'} \le 1$), while ε_{ii} quantifies the mean proportion of X_{ij} emigrating from community *i* towards some of the other communities in the metacommunity (and then $-1 \leq \varepsilon_{ii} \leq 0$). For consistency, we must have $| \varepsilon_{i'i'} | \geq \sum_{i \neq i'}^{I} \varepsilon_{ii'}$ for all i' = 1, ..., I; that is, biomass losses can occur during the dispersal process. The $\varepsilon_{ii'}$'s can vary as a function of the distance between communities, as well as their size, as traditionally considered in the theory of island biogeography and in metapopulation theory (Wilson and MacArthur 1967; Hanski and Ovaskainen 2000). Finally,

 $\{N_{ij}(dz, ds)\}_{j=1,...,J}^{i=1,...,J}$ is an independent and identically distributed (iid) sequence of Poisson measures, with intensity dzds, representing the stochastic dispersal regime of the species among communities. The movement of biomass will depend upon the species-dependent parameters b_j 's, so that for every i = 1, ..., I and j = 1, ..., J, $\int_{0}^{\infty} 1_{\{z \le b_j\}} N_{ij}(dz, \cdot) = N_{ij}([0, b_j], \cdot)$ is a Poisson process with instantaneous rate b_j . As the second line of (3) represents the discontinuous part of the process, the integral of the X_{ij} 's with respect to the Poisson measures is defined as in the usual Lebesgue-Stieltjes sense for right continuous processes with left limits, taking $X_{ij}(t-) = \lim_{s \uparrow t} X_{ij}(s)$.

This model describes the Lotka-Volterra type dynamics of J interacting species living in a spatially structured environment, such as an archipelago containing I islands or metacommunity, under two different and interacting dynamics: a continuous one, depicting growth, as well as intra and interspecific interactions between species, and a low frequency discrete one, describing the stochastic dispersal of species within the metacommunity. The model is general and can accommodate different scenarios, from assuming that all species and local communities are equal, to making the parameters characterizing the growth functions $f_{ii}(\cdot)$'s, such as carrying capacities and intrinsic growth rates, to be dependent on local communities and species attributes such as area, isolation, body size, and trophic status. The stochasticity of the model is due to the dispersal regime. Notice that, although the whole system is stochastic, there is no biomass transfer from and to the outside of the metacommunity. The model is general to the extent that it can be applied to multiple types of interactions; species can interact either through trophic or non-trophic interactions (e.g., competition, mutualism) or not at all (i.e., neutral).

Well-posedness of the model

In what follows we will show the well-posedness of this model and study its long-term behavior under standard assumptions. We begin by making explicit the assumptions of the model:

B(X, z) =

$$\begin{pmatrix} \varepsilon_{11}X_{11}1_{\{z \le b_1\}} \cdots \varepsilon_{1I}X_{I1}1_{\{z \le b_1\}} & 0 & \cdot & 0 \\ 0 & \cdot & \vdots \\ \vdots & & & 0 \\ 0 & & & \cdot & 0 & \varepsilon_{I1}X_{IJ}1_{\{z \le b_J\}} \cdots \varepsilon_{II}X_{IJ}1_{\{z \le b_J\}} \end{pmatrix}$$

- (A.1) The $X_{ij}(0)$'s are independent random variables with corresponding densities $\rho_{ij}(\cdot)$'s, all having compact support in \mathbb{R}_+ .
- (A.2) For each i = 1, ..., I and j = 1, ..., J, $f_{ij}(\cdot)$ is a $C^1(\mathbb{R})$ function.
 - Assumption (A.1) allows us to describe a plausible initial starting point for our system, since the limitations associated with the area occupied by the local community (e.g., an island) would only allow for a bounded amount of biomass, and (A.2) sets a typical condition of regularity.

In order to study the well-posedness of our model, we are going to write the whole dynamics of the system via matrices and vectors. Consider:

$$X = \begin{pmatrix} X_{11} \cdots X_{1J} \\ \vdots & \ddots & \vdots \\ X_{I1} \cdots & X_{IJ} \end{pmatrix},$$

$$N(dz, dt) = \begin{pmatrix} N_{11}(dz, dt) \cdots & N_{1J}(dz, dt) \\ \vdots & \ddots & \vdots \\ N_{I1}(dz, dt) \cdots & N_{IJ}(dz, dt) \end{pmatrix},$$

$$X = \operatorname{vec}(X) = \begin{pmatrix} X_{11} & X_{12} \cdots & X_{21} \cdots & X_{I(J-1)} & X_{IJ} \end{pmatrix}^{\mathrm{T}},$$

$$N(dz, dt) = \operatorname{vec}(N(dz, dt)^{\mathrm{T}})$$

$$= (N_{11}(dz, dt)N_{21}(dz, dt) \cdots N_{12}(dz, dt) \cdots N_{(I-1)J})$$

(dz, dt)N_{IJ}(dz, dt))^T,

$$F(\mathbf{X}) = (f_{11}(X_{11})f_{12}(X_{12})\cdots f_{21}(X_{21})\cdots f_{I(J-1)})$$
$$(X_{I(J-1)})f_{IJ}(X_{IJ}))^{\mathrm{T}},$$

$$\Lambda(X) = \operatorname{diag}\left(\sum_{j'=1}^{J} X_{1j'} \lambda_{1j'}; \sum_{j'=1}^{J} X_{1j'} \lambda_{2j'}; \cdots; \sum_{j'=1}^{J} X_{2j'} \lambda_{1j'}; \cdots; \sum_{j'=1}^{J} X_{Ij'} \lambda_{(J-1)j'}; \sum_{j'=1}^{J} X_{Ij'} \lambda_{Jj'}\right)$$

and

where vec(·) denotes the vectorization operator, T denotes the matrix transposition operator and diag $(a_1; \dots; a_n)$ denotes an $n \times n$ diagonal matrix whose elements therein are $a_1, ..., a_n$, respectively.

Thus, we have that X, F(X) and N(dz, dt) are $IJ \times 1$ vectors, and $\Lambda(X)$ and B(X, z) are $IJ \times IJ$ matrices. The dynamics of the system can thus be expressed as:

$$X(t) = X(0) + \int_{0}^{t} F(X(s))ds + \int_{0}^{t} \Lambda(X(s))X(s)ds$$
$$+ \int_{0}^{t} \int_{0}^{\infty} B(X(s-), z)N(dz, ds)$$
(4)

We have the following proposition.

Proposition 1 Under assumptions (A.1) and (A.2), the system (4) (and hence (3)) has a unique local solution, almost surely.

This proposition ensures only the existence of a unique local solution, that is, a unique well-posed solution when the state space of the process is limited (see proof in Appendix 1). This is so since there are cases for which our system can explode in a finite time. For example, consider an archipelago composed of a single island (I = 1) and thus with no dispersal, and inhabited by J = 2 species with a mutualistic relationship, i.e., λ_{12} and λ_{21} are positive, and with $f_j(x) = x(r_j - \alpha_j x)$ (notice that we have removed the subscript *i* since there is only one island in the system). Then, our system is given by the equations:

$$\begin{cases} \frac{dX_1(t)}{dt} = X_1(t)(r_1 - \alpha_1 X_1(t) + \lambda_{12} X_2(t)) \\ \frac{dX_2(t)}{dt} = X_2(t)(r_2 - \alpha_2 X_2(t) + \lambda_{21} X_1(t)) \end{cases}$$
(5)

From Mao et al. (2002) or Mao et al. (2003) we have that if $r_1 = r_2 = r \ge 1$, $\alpha_1 = \alpha_2 = \alpha$ and $\lambda_{12} = \lambda_{21} = \beta$ such that $\alpha^2 < \beta^2$, with initial conditions $X_1(0) = X_2(0) =$ $x_0 > 0$, system (5) can be reduced to the single deterministic differential equation:

$$\frac{dX(t)}{dt} = X(t)[r + (-\alpha + \beta)X(t)],$$

whose solution is:

$$X(t) = \frac{r}{-(-\alpha+\beta) + \frac{r+(-\alpha+\beta)x_0}{x_0} \exp\left\{-rt\right\}}$$

which explodes at time:

$$t = \frac{1}{r} \left(\ln(r + [-\alpha + \beta]x_0) - \ln([-\alpha + \beta]x_0) \right).$$

To avoid that (5) explodes at a finite time, it is required that $\lambda_{12}\lambda_{21} < \alpha_1\alpha_2$.

In our context, however, the system should not explode since biomass has an upper bound given by the finite area of the local communities or islands. Therefore, we must consider additional conditions in order to state a more appropriate well-posedness result for our model. First, consider that F(X) in (4) can be written as $F(X) = \tilde{F}(X)X$, where $\tilde{F}(X)$ is a $IJ \times IJ$ diagonal matrix. Define $\Gamma(X) = \tilde{F}(X) + \Lambda(X)$. Our system (4) can be now written as:

$$\mathbf{X}(t) = \mathbf{X}(0) + \int_{0}^{t} \Gamma(\mathbf{X}(s))\mathbf{X}(s)ds + \int_{0}^{t} \int_{0}^{\infty} B(\mathbf{X}(s-), z)\mathbf{N}(dz, ds).$$
(6)

Note that $\Gamma(X) = \text{diag}(\eta_1(X), ..., \eta_I(X))$, where each $\eta_i(X)$ is a $J \times J$ diagonal matrix. Finally, assume the following:

(A.3) There exists some $n \ge 0$ such that the diagonal matrix $\max_{i=1,...,l} \eta_i(X)$ is negative-definite if || X || > n.

If there were no dispersal (that is, if the dynamics of the species were only due to growth and competition processes), this last assumption makes it clear that the biomass of the species cannot escape a certain boundary. Then, the following proposition shows us that this property is also true when considering our stochastic dispersal component.

Proposition 2 Under assumptions (A.1), (A.2) and (A.3), the system (6) has a unique solution such that:

$$\sup_{t \in \mathbb{R}_{+}} \max_{i=1,...,I; j=1,...,J} X_{ij}(t) < \infty,$$
(7)

almost surely.

Also, if we assume that $|\varepsilon_{ii}| < 1$ and $\varepsilon_{ii'} > 0$, with $i \neq i'$, if $X_{ij}(0) > 0$ for some i = 1, ..., I and j = 1, ..., J, then $X_{ij}(t) > 0$ for any finite t > 0. See proof in Appendix 1.

Remark The last part of the above proposition tells us that if the $\varepsilon_{ii'}$'s do not take values on the boundary of their range, species extinction can only occur in the long term, the same characteristic shared by the classic (non-stochastic) general Lotka-Volterra model (see Hofbauer and Sigmund 1998). Notice that the initial condition can be $X_{ij}(0) = 0$, and for some t > 0, $X_{ij}(t) > 0$ due to dispersal. The essential issue here is that once the dynamics of $X_{ij}(\cdot)$ starts (i.e., with positive biomass), then the process can subsequently reach 0 only in the limit $t \to \infty$, unless $\varepsilon_{ii} = -1$ and $\varepsilon_{ii'} = 0$ for all $i' \neq i$. That is, it is possible to obtain extinction in finite time by manipulating the parameters $\varepsilon_{ii'}$'s in values on the boundary of their range. For example, consider the simple case of a single species (say, species 1) living in an isolated island (say, island 1) with no interactions with others species and emigration only. Then, if the initial condition is $X_{11}(0) = x_0 > 0$, its dynamics can be described as:

$$X_{11}(t) = x_0 + \int_0^t f_{11}(X_{11}(s))ds + \varepsilon_{11} \int_0^t \int_0^\infty X_{11}(s-) \mathbb{1}_{\{z \le b_1\}} N_{11}(dz, ds).$$

Notice that $\int_0^\infty 1_{\{z \le b_1\}} N_{11}(dz, \cdot)$ is a Poisson process with instantaneous rate b_1 . If $\varepsilon_{11} = -1$, then extinction occurs at $\tau_{11} = \inf\{t > 0 : \int_0^\infty 1_{\{z \le b_1\}} N_{11}(dz, t) > 0\}$, i. e., at the time of the first jump of N_{11} . We can also notice that this sudden extinction does not occur in its "analogous deterministic case", i. e., when the Poisson process is replaced by its rate:

$$\begin{aligned} x_{11}(t) &= x_0 + \int_0^t f_{11}(x_{11}(s))ds + \varepsilon_{11}b_1 \int_0^t x_{11}(s)ds \\ &= x_0 + \int_0^t f_{11}(x_{11}(s))ds - b_1 \int_0^t x_{11}(s)ds, \end{aligned}$$

which is a continuous dynamics, and therefore, cannot suddenly reach zero. However, such extreme situations will not be considered in this work.

Numerical analysis

Consider $f_{ij}(x) = r_j(1 - x/K_{ij})x$ in (3), where r_j is the intrinsic growth rate of species j and K_{ij} is the carrying capacity of species j in a local community or island i. Here, the term $-r_j/K_{ij}$ describes the effect of intraspecific competition on the growth of species. In the whole system (6), the elements of the diagonal of $\Gamma(X)$ are given by diag $(\eta_i(X)) = (r_1[1 - X_{i1}/K_{i1}] + \sum_{j'\neq 1} \lambda_{1j'}X_{ij'}, ..., r_J[1 - X_{iJ}/K_{iJ}] + \sum_{j'\neq J} \lambda_{Jj'}X_{ij'}),$ i = 1, ..., I. This example constitutes a generalized Lotka-Volterra system, where intrinsic growth is logistic, dispersal is presented as a stochastic regime, and which under (A.1)-(A.3) the whole biomass does not escape from a limited state space.

To understand the impact of the competition/colonization trade-off on species coexistence, as well as the impact of the spatial structure of the metacommunity on this trade-off, we consider a specific case with J = 2 competing species within a metacommunity containing I local communities:

$$\begin{aligned} X_{ij}(t) &= X_{ij}(0) + \int_{0}^{t} r_{j} \left(1 - \frac{X_{ij}(s)}{K_{ij}} \right) X_{ij}(s) ds \\ &+ \sum_{j'=1}^{2} \lambda_{jj'} \int_{0}^{t} X_{ij'}(s) X_{ij}(s) ds \end{aligned}$$

for i = 1, ..., I, j = 1, 2, and where $\lambda_{12}, \lambda_{21} < 0$ and $\lambda_{jj} = 0$.

In particular, we are interested in the scenario where one species is competitively dominant and the other is competitive inferior, such that in a closed system without dispersal, the dominant species will always exclude the inferior one. For an isolated community this condition can be expressed by the following relationships among parameter values $p_1 > r_2/r_1$ and $p_2 < r_1/r_2$, where $p_1 = -\lambda_{21}K_1/r_1$ and $p_2 = -\lambda_{12}K_2/r_2$ (notice that we remove the subscript *i* in the carrying capacity since this condition is valid for an isolated local community.

In Appendix 2, we recall the basic results of a twocompeting Lotka-Volterra system in a local community or a single island without dispersal.

In the following, we are going to show some cases in which dispersal causes changes in the phase plane (see Fig. 8 in Appendix 2) when we consider the dynamics given in (8). In particular, we will show a competition/colonization trade-off phenomenon, in which species in competition can coexist or reverse their advantage due to dispersal. However, we will start recalling some basic results about stability at equilibrium by considering *Lyapunov exponents*.

Stability

We can notice that **0** is an equilibrium solution of our system (6). In Proposition 2 we saw that if $X_{ij}(t) \neq 0$ for some $t \in \mathbb{R}_+$, i = 1, ..., I and j = 1, ..., J, the only possible way that $X_{ij}(\cdot)$ reaches 0 again (i.e., extinction of species j in local community i) is in the limit $t \rightarrow \infty$. In this regard, we can study the long-term persistence of some species within some local communities. One of the most popular methods to do this is through Lyapunov exponents. The aim is to know under which conditions extinction/persistence of some species within some communities will occur in the long term (e.g., Chesson 2018; Benaïm and Schreiber 2019).

We say that a process $\mathbf{Z}(\cdot)$ taking values in \mathbb{R}^d has a *Lyapunov exponent* ℓ if:

$$\ell = \limsup_{t \to \infty} \frac{1}{t} \log(\| \mathbf{Z}(t) \|) < \infty, \tag{9}$$

almost surely. If it exists, for a sufficiently large *t* we have that:

$$\| \mathbf{Z}(t) \| \le \xi \exp\{\ell t\},\tag{10}$$

almost surely, for a positive random variable ξ (see Applebaum 2009, Chapter 6, Section 6.8). Thus, as a way to distinguish the decay velocity, we will say that 0 is *almost* surely exponentially stable if $\ell < 0$.

For practical purposes, we are going to study the longterm behavior of observables of the form $g(\mathbf{x}) = u_{IJ}^{T}\mathbf{x}$, where u_{IJ} is an $IJ \times 1$ vector containing 1's and 0's depending on which species, over the *J* possible ones, and on which local communities among the *I* possible ones, we want to carry out our analysis.

Notice that our system (6) can be written as:

$$X(t) = X(0) + \int_{0}^{t} [\Gamma(X(s))X(s) + b(X(s))]ds + \int_{0}^{t} \int_{0}^{\infty} B(X(s-), z)M(dz, ds),$$
(11)

where $M(dz, ds) = N(dz, ds) - \mathbf{1}_{IJ}dzds$ is a martingale and $b(x) = \int_0^\infty B(x, z)\mathbf{1}_{IJ}dz$, with $\mathbf{1}_{IJ}$ the $IJ \times 1$ vector of 1's. Our aim here is to determine which components of $X(\cdot)$ will go to zero in the long term using Lyapunov exponents. Thus, we are interested in processes like:

$$\langle u_{IJ}, \boldsymbol{X}(t) \rangle = \langle u_{IJ}, \boldsymbol{X}(0) \rangle + \int_{0}^{t} \langle u_{IJ}, \Gamma(\boldsymbol{X}(s)) \boldsymbol{X}(s) + \boldsymbol{b}(\boldsymbol{X}(s)) \rangle ds$$

$$+\int_{0}^{t}\int_{0}^{\infty}\langle u_{IJ}, B(X(s-), z)M(dz, ds)\rangle, \qquad (12)$$

where u_{IJ} is an $IJ \times 1$ vector containing 1's and 0's and $\langle \cdot, \cdot \rangle$ is the scalar product. Define the operator $\mathcal{L}\langle u_{IJ}, \mathbf{x} \rangle := \langle u_{IJ}, \Gamma(\mathbf{x})\mathbf{x} + \mathbf{b}(\mathbf{x}) \rangle$. We have the following result.

Proposition 3 Under assumptions (A.1), (A.2) and (A.3), the process (12) has a Lyapunov exponent $\ell < \infty$. If additionally, there exists a constant c > 0 such that $\mathcal{L}\langle u_{IJ}, \mathbf{x} \rangle \leq -c \langle u_{IJ}, \mathbf{x} \rangle$, for all $\mathbf{x} \in \mathbf{R}$, then $\ell < 0$.

The proof of this proposition is provided in Appendix 1.

Remark Actually the condition to obtain a negative Lyapunov exponent can be replaced by $\mathcal{L}\langle u_{IJ}, X(t) \rangle \leq -c \langle u_{IJ}, X(t) \rangle$ almost surely, for a sufficiently large *t*.

However, the previous result is actually stronger, in the sense that there is an equivalence between extinction and the negativeness of ℓ , as stated in the following lemma.

Lemma 4 Under assumptions (A.1), (A.2) and (A.3), extinction holds whenever $\ell < 0$.

The proof of this Lemma is provided in Appendix 1.

Finally notice that, as a consequence of the boundedness of (6) (Proposition 2) and Lemma 4, we have that the case of non-extinction implies that the corresponding Lyapunov exponent results equal to zero.

Coexistence and the competition/colonization trade-off

To assess the existence and impact of the competition/colonization trade-off we first test the stability of the two species scenario, where species 1 is competitively dominant and species 2 is the inferior competitor, as a function of the dispersal rate of the inferior competitor (b_2). That is, we will consider a point where the classical Lotka-Volterra model for two species (without dispersal) has a unique stable equilibrium point, where one of the species go extinct.

Regarding the spatial structure, we will work first with one focal community and one refuge for the inferior competitor, defined as a local community where the dominant species cannot exist. To isolate the effect of dispersal with respect to the other parameters of the system, we will consider that species only differ in their competitive and dispersal abilities, but are otherwise identical, that is:

$$r_1 = r_2 = 1$$
, $K_{i1} = K_{i2} = 1$ (for all $i = 1, 2$),

The connectivity is given by the following choice of parameters

$$\varepsilon = \begin{pmatrix} 0.0 & 0.1 \\ 0.0 & -0.1 \end{pmatrix},$$

that is, dispersal only occur from community 2 to community 1, and on average the proportion of the biomass exchanged correspond to 0.1. A scheme of this simple architecture is presented in Fig. 1 (top).

The initial conditions for our simulations are

$$X_{11}(0) = 0.5, \quad X_{12}(0) = 0, \quad X_{21}(0) = 0.5,$$

 $X_{22}(0) = 0.5.$

In this scenario we assumed that the dominant competitor does not migrate, that is $b_1 = 0$ and analyze the long-term behavior of the dynamics for different values of b_2 , from 0.5 to 11 with incremental step 0.5. For each combination of parameters we performed 100 simulations and report the average biomass of species 2 on the local community where both species can potentially be found, we call this the focal community. The results of the model are shown in Fig. 2. One can see that the mean biomass of species 2 on the focal community increases as b_2 or dispersal from the refuge increases. The fraction of the carrying capacity of species 2 in the focal community reaches a maximum of about 0.8 at a dispersal rate b_2 between 4 and 5. However, as b_2 continues to increase, the mean biomass of species 2 decreases again.



The same effect is observed if we increase the competitive advantage of the superior competitor (Fig. 2), where we have repeated the numerical experiment for $p_1 = 2.5$ (i.e., $\lambda_{21} = -2.5$ and all other parameters stayed the same). We can observe a similar shape of the function, but much smaller absolute values (bottom). We conjecture that the concavity associated with the impact of dispersal on fostering coexistence is related to the relative differences between the dispersal/recovery time scales, implying that biomass is leaving the community faster than it is being replenished through growth.

In Fig. 3, we show the result of competition when the superior species (i.e., species 1) can only live in one community (community 1), and it cannot migrate; then, coexistence in community 1 is possible when species 2 can live in both communities and can migrate between them (Fig. 3, middle panels). Finally, when the dispersal rate of species 2 is much larger (Fig. 3, bottom panel) species 2 will go extinct from both communities because the time scale of dispersal is faster than that of recovery as discussed above. In Fig. 4 we can visualize the final outcome of the dynamics of both species in community 1 through the slope (in the long term) of the graph $log(X_{ij}(t))$ vs *t*, which corresponds to the (estimated) Lyapunov exponent.

Remark If we incorporate an Allee effect (e.g., Courchamp et al. 2008) to the model of interspecific interaction, we can observe more clearly the differences between the longterm behavior of the empirical mean of the trajectories and the trajectories themselves. Consider the following modification of the system (8):

$$X_{ij}(t) = X_{ij}(0) + \int_{0}^{t} r_{j} \left(1 - \frac{X_{ij}(s)}{K_{ij}}\right) \left(X_{ij}(s) - a\right) X_{ij}(s) ds$$
$$+ \sum_{j'=1}^{2} \lambda_{jj'} \int_{0}^{t} X_{ij'}(s) X_{ij}(s) ds$$
$$+ \sum_{i'=1}^{I} \varepsilon_{ii'} \int_{0}^{t} \int_{0}^{\infty} X_{i'j}(s -) \mathbb{1}_{\{z \le b_{j}\}} N_{i'j}(dz, ds),$$
(13)

with *a* the critical population density, or Allee threshold, below which the population growth rate becomes negative.



Fig. 2 Here we show how the proportional biomass of species 2 in the focal community changes when competing with species 1, the superior competitor according to the classical Lotka-Volterra model (without dispersal). We present a boxplot summarizing results from 100 simulations of the model, for a metacommunity with two local communities where the dispersal parameter of the subordinate species (i.e., species 2) varies. We considered the common parameters $r_1 = r_2 = 1$,

For simplicity, we consider the same Allee threshold (a=0.5%) for both species. Let X_{ij}^k be the *k*th simulated trajectory for species X_{ij} of a pool of *N* total simulations performed. We denote the empirical mean of the trajectories of species *i* on island *j* by $\bar{X}_{ij} = \frac{1}{N} \sum_{k=1}^{N} X_{ij}^k$. The time τ , is the time at which the population biomass X_{11}^k becomes smaller that the critical value *a*, and since the dynamics of X_{11} becomes strictly negative, an asymptotic extinction event occurs. The same conclusion holds true for X_{22} . For N = 1000 simulations performed, we calculate the first time when X_{11} (X_{22}) becomes smaller than a/2 and called that instant extinction time τ_1 (τ_2). The empirical mean and three trajectories are presented in Fig. 5 and the distribution of extinction times in Fig. 6. Approximately 30% (70%) of species 1 (species 2) trajectories do not go extinct up to the end of simulations (t = 600).

Effect of the metacommunity spatial structure

Finally, we assess the impact of the spatial structure, which affects which communities are connected and how intense that connection is depending on the distance between them, and of the number of communities in the metacommunity, on the competition/colonization trade-off under the scenario

 $K_{i1} = K_{i2} = 1$ (for i = 1 and i = 2). Connectivity parameters are given by $\varepsilon_{11} = \varepsilon_{21}$ equals 0 and $\varepsilon_{12} = -\varepsilon_{22} = 0.1$. The upper panel corresponds to $\lambda_{12} = -0.75$ and $\lambda_{21} = -1.25$, and the bottom panel corresponds to $\lambda_{12} = -0.75$ and $\lambda_{21} = -2.5$. In both cases we see an increase of the final biomass species 2 in the focal community, followed by a sudden decrease converging to 0 as b_2 further increases

of two species and *n*-communities, and where species 1 is dominant over species 2.

Regarding the spatial structure, we will work with different numbers of communities in a metacommunity, and also different number of refuges for the inferior competitor. To isolate the effect of spatial structure on the competition/colonization trade-off, over other parameters of the system, we will assume that species only differ in their dispersal and competitive abilities (i.e., $\lambda_{21} = -1.25$ and $\lambda_{12} = -0.75$) but are otherwise identical, thus $r_1 = r_2 = 1$, $K_{i1} = K_{i2} = 1$ (for all i).

First, to construct the connectivity matrix we fix a refuge community for the inferior species at coordinates (0, 0), and select randomly I-1 pairs (x_i, y_i) as locations for the other local communities in the metacommunity. We use a uniform $\mathcal{U}((-1, 1) \times (-1, 1))$ distribution for the selection. Next, we calculate the euclidean distance $d_{ii'}$ between any pair of local communities *i* and *i'* and make

$$\varepsilon_{ii'} = \begin{cases} -0.1 & \text{if } i = i', \\ 0 & \text{if } i = 1, i' \ge 2, \\ 0.1 \times \frac{\exp(-d_{ii'})}{\sum_{i' \neq i} \exp(-d_{ii'})} & \text{otherwise.} \end{cases}$$

The first condition implies that at each dispersal event, 10% of the species biomass leaves the local community of origin.

Fig. 3 Here we show the biomass dynamics of two species in two local communities and where species 1 is the superior competitor, according to the classical Lotka-Volterra model without dispersal. The three panels represents three cases of the dynamics of the two species in the two communities, where the dominant competitor (species 1) is restricted to community 1 and the inferior competitor (species 2) migrates at different rates bbetween local communities according to: (top) $b_2 = 0.1$; (center) $b_2 = 4.5$, and (bottom) $b_2 = 10$. We considered the common parameters $r_1 = 1$, $r_2 = 1, K_{i1} = 1, K_{i2} = 1$, for all i = 1, 2. Connectivity parameters are given by $\varepsilon_{11} = \varepsilon_{21} = 0$ and $\varepsilon_{12} = -\varepsilon_{22} = 0.1$. Also, $\lambda_{12} = -0.75$ and $\lambda_{21} = -1.25$ in (8) for all three cases



The second condition, that only the inferior competitor can inhabit the refuge community, while the third condition implies that the fraction of biomass dispersal between any two communities (not including the refuge) decreases with the distance between communities, hence most of the migrating biomass goes to close neighboring communities (see Fig. 1).

For the dispersal parameters, we take $b_1 = 1$ and vary b_2 from 0.5 to 11 with incremental step 0.5. We then study the competition/colonization trade-off of Fig. 2 as a function of the number of communities in the archipelago. For each number of communities I, we perform 100 simulations with randomly selected spatial configurations as we discussed previously. For each simulation, we calculate the average biomass of the inferior species over the communities excluding the refuge and for I = 3, 10 and I = 20. Here we observe that the total biomass of the inferior species decreases with I (Fig. 7). We finally studied the shape of the competition/colonization trade-off with I fixed but varying the number of refuges for the inferior competitor species.

As expected, we see that the biomass of the inferior species increases with the number of refuges.

Finally, in Appendix 3 we analyze the impact of the competition/colonization trade-off on the priority effects which corresponds to a scenario in model (8), in which the species that begins with higher initial biomass is the one that finally persists. There, we further study the effect of dispersal on persistence, showing that it can promote coexistence and a reversal of the initial advantage, depending on the intensity of dispersal, further emphasizing the importance of the competition/colonization trade-off and the complexity of species coexistence.

Discussion

The role of dispersal in fostering coexistence in metacommunities, and in particular the competition/colonization trade-off, has been widely reported. The processes and mechanisms that affect its intensity, however, are less well

Fig. 4 The convergence of Lyapunov exponents of species 1 and species 2 in community 1 for the corresponding cases of Fig. 3, from top to bottom. In solid line is depicted one typical trajectory and in dashed line we have a mean of 100 trajectories, where we can see a smoothed version of $log(X_{ij}(t))$ vs t. The slopes of the long-term tendencies tell us the long-term fate of species; slope ≈ 0 will mean persistence and negative slope indicates extinction. Parameters are the same as used in Fig. 3



known. In this contribution, we have shown that the species colonization trade-off is an important coexistence mechanism, that this effect is a concave function of the dispersal rate, and that it varies in magnitude as a function of the topology or spatial arrangement of local communities, and the number of refuges for the inferior competitor and that it can reverse priority effects fostering coexistence even when no competitive hierarchy exists. Modern coexistence theory emphasizes at its core, that coexistence is possible whenever fitness differences are smaller than niche differences (Chesson 2018), our results highlight the importance of additional mechanisms related to the topology of the system of communities as well as its relationship with dispersal in affecting coexistence (see also Schreiber and Killingback 2013).

Under the competition/colonization trade-off it is clear that coexistence in a local community will be most effective if local habitat patches are continually disturbed, otherwise, the superior competitor could slowly reach everywhere excluding the inferior competitor. This has been shown by the experimental addition of an increasing number of seeds of different species in the pool to an experimental plot, which usually results in an increase in the relative abundance of large-seeded species, which is in agreement with the idea that large-seeded species are poor dispersers but strong competitors (Turnbull et al. 1999). At the level of metacommunities, the continuous disturbance or removal of local communities seems unrealistic, at least for macroorganisms, this is why we included a refuge for the inferior competitor or a local community where the superior competitor is unable to arrive. This could reflect a local community that it is not reachable because of distance (e.g., dispersal limitation) or because it has a particular combination of characteristics that render it unsuitable for the superior competitor. This spatial niche segregation is known to foster coexistence and could reflect a tradeoff between dispersal ability and ecological specialization Jocque et al. (2010) as well as the effects of dispersal or recruitment limitation (Hubbell 2005). In this regard, our results concur with the observation that the regional dimension of species interactions could promote the local coexistence of competing species as a consequence of **Fig. 5** Expected value for the proportional biomass (top) and three different trajectories of the corresponding cases of Fig. 3 with Allee effect. We show trajectories up to time 200 only



patch heterogeneity at a regional scale (e.g., Levin 1974; Amarasekare and Nisbet 2001).

It is interesting that the nature of the competition/colonization trade-off is such that the higher the dispersal the more difficult it becomes to replace the lost biomass with local growth, which is diluted as the number of local communities increases, such that the species becomes increasingly rare in abundance an effect that is counterbalanced by an increase in the number of refuges (Figs. 2 and 7). The fact that intermediate dispersal fosters coexistence and thus diversity agrees with other evidence (e.g., Cadotte 2006; Venail et al. 2008). In particular, Venail et al. (2008) experimentally show that intermediate dispersal maximizes diversity and productivity, as selection at intermediate rates of dispersal leads to niche differentiation as well as to a better coverage of the heterogeneity of the environment. In an evolutionary context, this in turn could lead to the expression of a dispersal-specialization trade-off, and to priority effects if the first species arriving at a patch is able to adapt to the local conditions (De Meester et al. 2016).

Priority effects arise when the presence or absence of different species in a local community depends on the order



Fig. 6 Distributions of extinction times for species 1 in community 1 and species 2 in community 2 for the corresponding system with Allee effect in Fig. 5

in which they arrive and establish, and their initial density. In ecological terms, this regime is what it is expected under Lotka-Volterra competition with both species with competitive coefficients α larger than 1, such that the result of competition depends on initial conditions. In this regime it has been shown that dispersal fosters coexistence along a limited range of dispersal intensities, and that diversity decreases as dispersal further increases, disappearing the priority effect. Mohd et al. (2016) shows using a spatially extended Lotka-Volterra competition model with a diffusion term, that the disappearance of priority effects is associated with a saddle node bifurcation. We show a similar result

whereby dispersal can reverse the priority effect or foster coexistence under a limited range of dispersal rates.

Stochasticity in dispersal have been previously considered from different perspectives in modeling: from a macro-scale, at the level of species, where colonization and extinction follow a birth-death processes (see, e.g., MacArthur and Wilson 1963; Wilson and MacArthur 1967; Hanski and Ovaskainen 2000); and from gene frequency ("micro-scale", see Nagylaki 1979), where genes migrate at random and stochasticity is considered within the dispersal rates themselves at each time step. In this sense, our model situates dispersal from an "intermediary" scale.

Fig. 7 Effects of the number of local communities I and refuges on the coexistence of species in a metacommunity. (Upper panel) Impact of the number of local communities on the strength of the competition/colonization trade-off. In blue I = 3, in red I = 10 and in yellow I = 20. In all cases the number of refuges is 1. (Bottom panel) competition/colonization trade-off as a function of the number of refuges for a fixed number of local communities I = 10: in blue 10% of the communities correspond to refuges, in red 20%, in yellow 30%, and in violet 40%. In green, the case without refuges. Parameters used are described in the main text



Species biomass is the unit considered here, and the stochastic dispersal regime refers to "biomass flows" at stochastic random jumps, according to a Poisson regime, similar to the birth-death processes as represented by (2).

One of the important characteristics of our model resides in its generality. This is manifested in the fact that it can be used to analyze entire networks of interspecific interactions from food webs (e.g., Holt 1996; Holt et al. 2005; Holt 2009) to metafoodwebs and metaecosystems (Gravel et al. 2016; Brechtel et al. 2019) that are usually modeled using deterministic approaches to the inclusion of higher-order interactions, which are known to affect coexistence (e.g., Saavedra et al. 2017; Singh and Baruah 2020). Further, our model can be applied to the wider class of models that address collective behavior, which can be found in diverse areas such as decision-making (see Seeley et al. 2012) or epidemiological models (see Murray 2007). In fact, it belongs to the broad category of models that incorporate discontinuous dynamical processes. The notation we use in (3) resembles those used by Nicolas Fournier and Eva Löcherbach (see De Masi et al. 2015; Fournier and Löcherbach 2016), where they propose a microscopic model for a system of interacting neurons with linear dynamics and action potentials that are modeled as jumps directed by Poisson measures. On that system, the hydrodynamic limit and its properties are studied. A similar situation is found in the structured age model of interacting neurons proposed by Pakdaman, Perthame and Salort (see Pakdaman et al. 2009, 2013; Quininao and Touboul 2015) where again the hydrodynamic limits are deduced from the microscopic point of view. It is important to highlight that in all these studies, the analysis is made in the context of large particle systems, and therefore the description in terms of the mean-field limits is possible (see, e.g., Ha and Liu 2009; Haskovec 2013). In our case, we have focused the analysis on those situations where the presence of a discontinuous jumps process impact on the stability of steady points for deterministic dynamics as the example presented for a competitive Lotka-Volterra system. We acknowledge that our results should resemble those observed under a deterministic framework since the deterministic formulation corresponds to the expected dynamics (see Fig. 5 upper panel), but the stochastic approach is much richer, as many trajectories can go to extinction even is the long-term expected behavior is coexistence and the opposite is also true. This can be clearly seen if we introduce an Allee effect (Fig. 5), giving rise to a right-skewed distribution of extinction times (Fig. 6). The existence of stochasticity implies that, in practice, it is difficult, if not impossible, to discern the strength and the competitive abilities of species from observing a time series of pairs of interacting species (see also Freilich et al. 2020), as different results can be observed even if the most likely is compatible with the deterministic dynamics.

One of the novel aspects of our stochastic model of metacommunities is associated with our use of a stochastic dispersal that follows a jump Poisson process. There are, however, several ways to introduce dispersal stochasticity in models of interacting species. Recently, for example, Hening et al. (2018) developed a stochastic population model in spatially heterogeneous environments, where the flow evolves in a patchy habitat according to a drift term associated with a density-dependent intrinsic growth function, dispersal, and a diffusive Brownian term. Including stochasticity via a component that affects in the same scale of the continuous growth, as made in Hening et al. (2018) (see also Mao et al. 2002; Mao et al. 2003; Cattiaux and Méléard 2010), is quite common, and in our case it would be equivalent to introduce additionally in (4) a stochastic continuous diffusion term of the form $\int_0^l \sigma(X(s)) dW(s)$ where for all $x \in \mathbb{R}^{IJ}$, $\sigma(\mathbf{x})$ is a $IJ \times r$ positive semi-definite matrix and $W(\cdot)$ is a $r \times 1$ Brownian motion, for some r > 1 (see also the recent work by Rebolledo et al. (2019) in which, under the context of stochastic open network models in ecology, dynamic biomass flows are stochastically affected by the environment by means of high and low noise frequencies, described through Brownian and Poisson noises respectively). Under this scenario, it can be shown that our results can remain unchanged (except probably for the boundedness result of Proposition 2) when the matrix function $a(\cdot, \cdot)$ defined by $a(\mathbf{x}, \mathbf{y}) = \sigma(\mathbf{x})\sigma(\mathbf{y})^{\mathrm{T}}$ for all $x, y \in \mathbb{R}^{IJ}$, is, e.g., bi-Lipschitz continuous (see Applebaum 2009, Section 6.2). Nevertheless, such a boundedness is a mathematically technical subtlety since the resulting diffusive process will be almost sure finite within each finite time horizon, and the probability that the biomass escapes from a "large compact" is actually small. If we want to avoid this mathematical inconvenient when considering a continuum noise term, we might set "borders in the diffusion", which would keep the boundedness property (see, e.g., Skorokhod 1961, 1962; Lions and Sznitman 1984; Tanaka 2002). However, we leave this issue for future work.

In summary, our framework allows for a simple way of including stochasticity in generalized models of species interactions, with the capability of analyzing simultaneously different kinds of interactions including whole food webs in spatially structured environments (e.g., Pillai et al. 2011; Plitzko and Drossel 2015; Barter and Gross 2017) and include, at the same time, dynamics at two scales; a continuous one representing the scale of species demography and interactions and a low frequency one representing stochastic dispersal. Our model has the potential to be extended to analyze other relevant processes at the level of metacommunities such as climate change, which can greatly affect the species persistence (see, e.g., Zhou and Kot 2011; Tejo et al. 2017), as well as habitat degradation, destruction, and restoration in a stochastic framework. It is general enough to be able to deal with the complexity of multi-species interactions in stochastic environments.

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Data availability Not applicable.

Code availability All codes used in the simulations are available upon request.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Appendix 1. Proofs

Proof of Proposition 1

Let $\|\cdot\|$ be the usual Euclidean norm in \mathbb{R}^d , and for real matrices $Q = (q_{lk})_{l,k=1,..,d}$ define the norm $\|\cdot\|_{\max}$ as $\|Q\|_{\max} = \max_{1 \le l,k \le d} |q_{lk}|$. Notice that for an \mathbb{R}^d -vector Y, we have $\|QY\| \le \sqrt{d} \|Q\|_{\max} \|Y\|$. Let $\mathbf{x} \in \mathbb{R}^{IJ}$. Then, we have the following inequalities: $\|\Lambda(\mathbf{x})\mathbf{x}\| \le \sqrt{IJ} \| \Lambda(\mathbf{x})\|_{\max} \|\mathbf{x}\|$ and $\|B(\mathbf{x}, z)\| = \|\operatorname{vec}(B(\mathbf{x}, z))\| \le \sqrt{IJ} \|B(\mathbf{x}, z)\|_{\max} \le \sqrt{IJ} \|\beta(z)\|_{\max} \|\mathbf{x}\|$, where

$$\beta(z) = \begin{pmatrix} \varepsilon_{11} \mathbf{1}_{\{z \le b_1\}} \cdots \varepsilon_{1I} \mathbf{1}_{\{z \le b_1\}} & 0 \cdots & 0 \\ 0 & \cdot & \vdots \\ \vdots & \cdot & 0 \\ 0 & \cdot & 0 & \varepsilon_{I1} \mathbf{1}_{\{z \le b_I\}} \cdots \varepsilon_{II} \mathbf{1}_{\{z \le b_I\}} \end{pmatrix}.$$
(14)

Using those inequalities, we have that:

$$D(\mathbf{x}) = \| F(\mathbf{x}) \|^{2} + \| \Lambda(\mathbf{x})\mathbf{x} \|^{2} + \int_{0}^{\infty} \| B(\mathbf{x}, z) \|^{2} dz$$

$$\leq \| F(\mathbf{x}) \|^{2} + IJ \| \Lambda(\mathbf{x}) \|_{\max}^{2} \| \mathbf{x} \|^{2}$$

$$+ IJ \int_{0}^{\infty} \| \beta(z) \|_{\max}^{2} dz \| \mathbf{x} \|^{2}$$

 $\leq K(\boldsymbol{x})(1+ \parallel \boldsymbol{x} \parallel^2),$

where $K(\mathbf{x}) = \max\{ \| F(\mathbf{x}) \|^2, IJ \| \Lambda(\mathbf{x}) \|_{\max}^2, IJ \int_0^\infty \| \beta(z) \|_{\max}^2 dz \}$. By (A.1), $\| X(0) \|$ is bounded, so we can choose a large $K_0 \gg K(X(0))$ such that $D(\mathbf{x}) \le K_0(1+\| \mathbf{x} \|^2)$, for all \mathbf{x} belonging to the set $\{\mathbf{x} \in \mathbb{R}^{IJ} : K(\mathbf{x}) \le K_0\}$. This means that (4) has a local linear growth.

On the other hand, by (A.2) $F(\cdot)$ is a locally Lipschitz function. Let $L(\mathbf{x}) = \Lambda(\mathbf{x})\mathbf{x}$, for all $\mathbf{x} \in \mathbb{R}^{IJ}$. Now, note that for any $\mathbf{x}, \mathbf{y} \in \mathbb{R}^{IJ}$ we have that $L(\mathbf{x}) - L(\mathbf{y}) =$ $[\Lambda(\mathbf{x}) + \Lambda(\mathbf{y})][\mathbf{x} - \mathbf{y}]/2 + [\Lambda(\mathbf{x}) - \Lambda(\mathbf{y})][\mathbf{x} + \mathbf{y}]/2$, and then, $|| L(\mathbf{x}) - L(\mathbf{y}) || \le (\sqrt{IJ}/2) || \Lambda(\mathbf{x}) + \Lambda(\mathbf{y}) ||_{\max} ||$ $\mathbf{x} - \mathbf{y} || + (\sqrt{IJ}/2) || \Lambda(\mathbf{x}) - \Lambda(\mathbf{y}) ||_{\max} || \mathbf{x} + \mathbf{y} ||$, where

$$\| \Lambda(\mathbf{x}) - \Lambda(\mathbf{y}) \|_{\max} = \max_{i,j} |\sum_{j'=1}^{J} (x_{ij'} - y_{ij'})\lambda_{jj'}|$$

$$\leq \sum_{i'=1}^{I} \sum_{j'=1}^{J} |x_{ij'} - y_{ij'}|| \lambda_{jj'}|$$

$$\leq \parallel \mathbf{x} - \mathbf{y} \parallel \sqrt{I \sum_{j'=1}^{J} |\lambda_{jj'}|^2}$$

by Hölder inequality. That is,

$$\| L(\mathbf{x}) - L(\mathbf{y}) \| \leq \frac{\sqrt{IJ}}{2} \left(\| \Lambda(\mathbf{x}) + \Lambda(\mathbf{y}) \|_{\max} + \| \mathbf{x} + \mathbf{y} \| \sqrt{I \sum_{j'=1}^{J} |\lambda_{jj'}|^2} \right) \| \mathbf{x} - \mathbf{y} \|,$$

and thus for any $x, y \in \mathbb{R}^{IJ}$ such that $||x|| \vee ||y|| \leq M$, where *M* is a constant such that $M \gg ||X(0)||$, there exists a constant H_M such that $||L(x) - L(y)|| \leq H_M ||x - y||$. So, it means that $L(\cdot)$ is locally Lipschitz as well. Therefore, conditions of Theorem 9.1 in Chapter IV from Ikeda and Watanabe (2014) (linear growth and Lipschitz conditions) are locally satisfied, and hence, we have existence and uniqueness of a local solution. \Box

Proof of Proposition 2

Recalling the formulation $X_{ij}(t)$ of (3), we define the following quantity:

$$Y_j(t) := \sum_{i=1}^{I} X_{ij}(t),$$
(15)

which models the total biomass of species j over the whole system (i.e., archipelago) at time t. We recall that no biomass is transferred from outside the archipelago and all the emigrant biomass of any species in any community at most lands over some of the other communities. Therefore, the stochastic part of (3) must satisfy:

$$\sum_{i=1}^{I} \sum_{i'=1}^{I} \varepsilon_{ii'} \int_{0}^{t} X_{i'j}(s-) \int_{0}^{\infty} \mathbb{1}_{\{z \le b_j\}} N_{i'j}(dz, ds)$$

=
$$\sum_{i'=1}^{I} \left(\sum_{i=1}^{I} \varepsilon_{ii'} \right) \int_{0}^{t} X_{i'j}(s-) \int_{0}^{\infty} \mathbb{1}_{\{z \le b_j\}} N_{i'j}(dz, ds) \le 0,$$

(16)

almost surely, since $\sum_{i=1}^{I} \varepsilon_{ii'} \leq 0$ for any i'. Let $Y = (Y_1, ..., Y_J)^T$. Now, in (6), let Ξ be the $J \times IJ$ matrix such that $\Xi X = Y$. We have that:

$$\mathbf{Y}(t) \leq \mathbf{Y}(0) + \int_{0}^{t} \Xi \Gamma(\mathbf{X}(s)) \mathbf{X}(s) ds,$$

by (16). Then we get:

$$Y(t) \leq Y(0) + \int_{0}^{t} \Xi \Gamma(X(s)) X(s) ds \leq Y(0)$$
$$+ \int_{0}^{t} \max_{i=1,\dots,I} \eta_i(X(s)) \Xi X(s) ds$$

$$= \mathbf{Y}(0) + \int_{0}^{t} \max_{i=1,\dots,I} \eta_i(\mathbf{X}(s))\mathbf{Y}(s)ds.$$

By (A.3), it is clear that $\sup_{t \in \mathbb{R}_+} \max_{j=1,...,J} Y_j(t) < \infty$, almost surely, and (7) follows from the fact that $\max_{j=1,...,J} Y_j(\cdot) \ge \max_{i=1,...,I; j=1,...,J} X_{ij}(\cdot)$, almost surely.

Now, we shall prove that extinction occurs in the long term. First, notice that under structural assumptions made in (6), we can write in (3) $f_{ij}(x)$ in the form $\tilde{f}_{ij}(x)x$.

Therefore, for any $t \in \mathbb{R}_+$, i = 1, ..., I and j = 1, ..., J we have:

$$\begin{split} X_{ij}(t) &\geq X_{ij}(0) + \int_{0}^{t} \tilde{f}_{ij}(X_{ij}(s))X_{ij}(s)ds \\ &+ \int_{0}^{t} \sum_{j' \neq j}^{J} \lambda_{jj'}X_{ij'}(s)X_{ij}(s)ds \\ &- \int_{0}^{t} X_{ij}(s) \int_{0}^{\infty} \mathbb{1}_{\{z \leq b_{j}\}} N_{ij}(dz, ds) \\ &= X_{ij}(0) + \int_{0}^{t} \tilde{f}_{ij}(X_{ij}(s))X_{ij}(s)ds \\ &+ \int_{0}^{t} \sum_{j' \neq j}^{J} \lambda_{jj'}X_{ij'}(s)X_{ij}(s)ds \\ &- \int_{0}^{t} X_{ij}(s)b_{j}ds + \int_{0}^{t} X_{ij}(s)\mathcal{M}_{ij}([0, b_{j}], ds), \end{split}$$

where $\mathcal{M}_{ij}([0, b_j], t) = -(\int_0^\infty \mathbf{1}_{\{z \le b_j\}} N_{ij}(dz, t) - tb_j) = tb_j - N_{ij}([0, b_j], t)$ is a square-integrable martingale. This implies that:

$$\begin{aligned} X_{ij}(t) &\geq X_{ij}(0) \exp\left\{\int_0^t \left[\tilde{f}_{ij}(X_{ij}(s)) + \sum_{j' \neq j}^J \lambda_{jj'} X_{ij'}(s) - b_j\right] ds + \mathcal{M}_{ij}([0, b_j], t) \right\} \end{aligned}$$

$$\geq X_{ij}(0) \exp\left\{t \inf_{\mathbf{x}\in R^J} G_{ij}(\mathbf{x}) + \mathcal{M}_{ij}([0, b_j], t)\right\},\$$

where

$$\inf_{\mathbf{x}\in R^J} G_{ij}(\mathbf{x}) := \inf_{(x_1,\dots,x_J)^{\mathrm{T}}\in R^J} \left[\tilde{f}_{ij}(x_j) + \sum_{j'\neq j}^J \lambda_{jj'} x_{j'} - b_j \right],$$

and R^J is the bounded subset of \mathbb{R}^J_+ which delimits the state space of $(X_{i1}(\cdot), ..., X_{iJ}(\cdot))^T$ for any i = 1, ..., I. On the other hand, we have that:

$$\mathbb{E}\left(\exp\left\{\mathcal{M}_{ij}([0, b_j], t)\right\}\right) = \exp\left\{b_j t \exp\{-1\}\right\},\$$

and thus,

$$\mathbb{E}(X_{ij}(t)) \ge \mathbb{E}(X_{ij}(0)) \exp\left\{t (\inf_{\mathbf{x} \in R^J} G_{ij}(\mathbf{x}) + b_j \exp\{-1\})\right\}.$$
(17)

Notice that it must satisfy $b_j \exp\{-1\} + \inf_{x \in \mathbb{R}^J} G_{ij}(x) \le 0$ if $X_{ij}(0) > 0$, since otherwise $\mathbb{E}(X_{ij}(t)) \to \infty$ when $t \to \infty$, which contradicts the fact that $X_{ij}(\cdot)$ is bounded. So, if $X_{ij}(0) > 0$, exp $\{t \inf_{\mathbf{x} \in \mathbb{R}^J} G_{ij}(\mathbf{x}) + \mathcal{M}_{ij}([0, b_j], t)\}$ never reaches zero in finite time, and then neither does $X_{ij}(\cdot)$. \Box

Proof of proposition 3

First notice that the vector $\boldsymbol{b}(\boldsymbol{x})$ can be decomposed into $\boldsymbol{b}(\boldsymbol{x}) = \boldsymbol{\beta}\boldsymbol{x}$, where $\boldsymbol{\beta} = \int_0^\infty \beta(z)dz$ and $\beta(z)$ is the $IJ \times IJ$ matrix defined in (14). Also, we have that $|| B(\boldsymbol{x}, z) || \le \sqrt{IJ} || \beta(z) ||_{\max} || \boldsymbol{x} ||$.

We start by showing the existence of a Lyapunov exponent for (6). Consider its representation given by (11). According to Theorem 6.8.2 in Applebaum (2009), we have to show that the alternative condition to the Assumption 6.8.1, given in Equation (6.42), is satisfied for our system (11) for all $\mathbf{x} \in \mathbf{R}$. That is, the existence of a positive constant L' such that $\mathbf{x}^{\mathrm{T}}\Gamma(\mathbf{x})\mathbf{x} + \mathbf{x}^{\mathrm{T}}\mathbf{b}(\mathbf{x}) + \int_{0}^{\infty} || B(\mathbf{x}, z) ||^{2} dz \le L'(1+||\mathbf{x}||^{2})$. In fact, by the above, we have that:

$$\mathbf{x}^{\mathrm{T}}\Gamma(\mathbf{x})\mathbf{x} + \mathbf{x}^{\mathrm{T}}\mathbf{b}(\mathbf{x}) + \int_{0}^{\infty} \|B(\mathbf{x}, z)\|^{2} dz \leq \mathbf{x}^{\mathrm{T}}\Gamma(\mathbf{x})\mathbf{x}$$
$$+ \mathbf{x}^{\mathrm{T}}\boldsymbol{\beta}\mathbf{x} + IJ \|\mathbf{x}\|^{2} \int_{0}^{\infty} \|\beta(z)\|_{\max}^{2} dz \leq L'' \|\mathbf{x}\|^{2},$$

where $L'' = \max\{\sup_{x \in \mathbb{R}} \Gamma(x), \| \beta \|, IJ \int_0^\infty \| \beta(z) \|_{\max}^2 dz\}$. Clearly it also implies that the process (12) has a Lyapunov exponent.

Now, consider that there exists a constant c > 0 such that $\mathcal{L}\langle u_{IJ}, \mathbf{x} \rangle \leq -c \langle u_{IJ}, \mathbf{x} \rangle$ for all $\mathbf{x} \in \mathbf{R}$. Define $\mathbb{E}_{\mathbf{x}}(\langle u_{IJ}, \mathbf{X}(t) \rangle) := \mathbb{E}(\langle u_{IJ}, \mathbf{X}(t) \rangle \mid \mathbf{X}(0) = \mathbf{x})$, for all $t \in \mathbb{R}_+$. Applying it to (12) we obtain:

$$\mathbb{E}_{\mathbf{x}}(\langle u_{IJ}, \mathbf{X}(t) \rangle) = \langle u_{IJ}, \mathbf{x} \rangle + \int_{0}^{t} \mathbb{E}_{\mathbf{x}}(\langle u_{IJ}, \Gamma(\mathbf{X}(s)) \mathbf{X}(s) + \mathbf{b}(\mathbf{X}(s)) \rangle) ds$$

$$\leq \langle u_{IJ}, \mathbf{x} \rangle - c \int_{0}^{t} \mathbb{E}_{\mathbf{x}}(\langle u_{IJ}, \mathbf{X}(s) \rangle) ds.$$

Then, by Gronwall's inequality we get:

$$\mathbb{E}_{\boldsymbol{x}}(\langle u_{IJ}, \boldsymbol{X}(t) \rangle) \leq \langle u_{IJ}, \boldsymbol{x} \rangle \exp\{-ct\},\$$

which implies that $\langle u_{IJ}, X(\cdot) \rangle$ goes exponentially fast to 0.

Proof of Lemma 4

For a chosen u_{IJ} , there exists i' = 1, ..., I and j' = 1, ..., J such that $\mathbb{E}_{\mathbf{x}}(X_{i'j'}(\cdot)) \leq \mathbb{E}_{\mathbf{x}}(\langle u_{IJ}, \mathbf{X}(\cdot) \rangle)$, where $\mathbb{E}_{\mathbf{x}}(X_{i'j'}(\cdot))$ satisfies (17) for i = i' and j = j' given $X_{i'j'}(0) = \mathbf{x}$. Therefore, extinction can only occur in an exponentially fast way. \Box

Appendix 2. Some results of a classical competitive Lotka-Volterra system

In the present appendix we recall some results of a classical competitive Lotka-Volterra system and its corresponding parameter space, in order to enlighten the long-term solutions and the reader realize how the presence of dispersal can transform such parameter space and bifurcation diagrams. Notice that as we will start treating the classic case, in a local community without dispersal, first we do not consider the subscript *i*. Consider then the equations:

$$\begin{aligned} x_1'(t) &= x_1(t) \left(r_1 + \alpha_{11} x_1(t) + \alpha_{12} x_2(t) \right), \\ x_2'(t) &= x_2(t) \left(r_2 + \alpha_{21} x_1(t) + \alpha_{22} x_2(t) \right). \end{aligned}$$

For any steady state (x_1, x_2) , the eigenvalues of the Jacobian matrix are given by:

$$\frac{1}{2}\left(\operatorname{tr}(J) \pm \sqrt{\operatorname{tr}(J)^2 - 4\operatorname{det}(J)}\right),\,$$

where tr(J) and det(J) stand for the trace and determinant of the matrix

$$J = \begin{pmatrix} r_1 + 2\alpha_{11}x_1 + \alpha_{12}x_2 & \alpha_{12}x_1 \\ \alpha_{21}x_2 & r_2 + \alpha_{21}x_1 + 2\alpha_{22}x_2 \end{pmatrix}.$$

In the following we simply write T = tr(J) and D = det(J). The standard trace-determinant analysis tells us that

- Case 4 det(J) > tr(J)²: the system has two complex eigenvalues, If tr(J) < 0 then the steady state is stable. On the other hand, if tr(J) > 0 then the steady state is unstable.
- Case det(*J*) < 0: in this scenario, both eigenvalues are positive and have different sign, thus the steady state is unstable.
- Case $0 < 4 \det(J) < \operatorname{tr}(J)^2$: if $\operatorname{tr}(J) > 0$ then the two eigenvalues are positive and the steady state is unstable. Otherwise, $\operatorname{tr}(J) < 0$ then the configuration is asymptotically stable.

Recall also that steady states are either (0, 0), $(0, -r_2/\alpha_{22})$, $(-r_1/\alpha_{11}, 0)$ or

$$\bar{x}_1 = rac{-r_1 lpha_{22} + r_2 lpha_{12}}{lpha_{11} lpha_{22} - lpha_{12} lpha_{21}}, \quad \bar{x}_2 = rac{-r_2 lpha_{11} + r_1 lpha_{21}}{lpha_{11} lpha_{22} - lpha_{12} lpha_{21}}$$

Then we have:

- (0, 0): it follows that $T = r_1 + r_2$ and $D = r_1r_2$, in which case the extinction scenario is unconditionally unstable.
- $(0, -r_2/\alpha_{22})$: we have

$$T = r_1 - r_2 \frac{\alpha_{12}}{\alpha_{22}} - r_2$$
 and $D = -r_2 \left(r_1 - r_2 \frac{\alpha_{12}}{\alpha_{22}} \right)$.

Stability of this fixed point is reduced to the condition

$$r_1 < r_2 \frac{\alpha_{12}}{\alpha_{22}}$$

• $(-r_1/\alpha_{11}, 0)$: similarly,

$$T = -r_1 + r_2 - r_1 \frac{\alpha_{22}}{\alpha_{11}}$$
 and $D = -r_1 \left(r_2 - r_1 \frac{\alpha_{21}}{\alpha_{11}} \right)$,

by consequence, the stability of this fixed point holds true if and only if

$$r_2 < r_1 \frac{\alpha_{21}}{\alpha_{11}}.$$

• (\bar{x}_1, \bar{x}_2) : it follows that

$$T = \alpha_{11}\bar{x}_1 + \alpha_{22}\bar{x}_2$$
 and $D = (\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21})\bar{x}_1\bar{x}_2$,

the existence and stability of this final fixed point is only under the conditions

 $\alpha_{11}\alpha_{22} > \alpha_{12}\alpha_{21}, \quad r_1\alpha_{22} < r_2\alpha_{12} \quad \text{and} \quad r_2\alpha_{11} < r_1\alpha_{21}.$

Notice that, since $\alpha_{ii} < 0$ then second and third conditions are equivalent to

$$r_1 > r_2 \frac{\alpha_{12}}{\alpha_{22}}$$
 and $r_2 > \frac{r_1 \alpha_{21}}{\alpha_{11}}$,

thus we have the instability of all previous scenarios.

Analysis of the phase plane

If we come back to the numerical example with 2 species in a local community without dispersal, the system of equations are:

$$\begin{aligned} x_1'(t) &= x_1(t) \left(r_1 - \frac{r_1}{K_1} x_1(t) + \lambda_{12} x_2(t) \right), \\ x_2'(t) &= x_2(t) \left(r_2 + \lambda_{21} x_1(t) - \frac{r_1}{K_2} x_2(t) \right), \end{aligned}$$

thus defining the interacting matrix

$$\left(\begin{array}{cc} -r_1/K_1 & \lambda_{12} \\ \lambda_{21} & -r_1/K_2 \end{array}\right).$$

Parameters r_j 's are intrinsic for each species, thus we can consider them as fixed. Therefore, we can make an analysis of the stability of the fixed points under the two nonnegative quantities:

$$p_1 = \frac{\alpha_{21}}{\alpha_{11}}, \qquad p_2 = \frac{\alpha_{12}}{\alpha_{22}},$$

where $\alpha_{21} = \lambda_{21}$, $\alpha_{12} = \lambda_{12}$, $\alpha_{11} = -r_1/K_1$ and $\alpha_{22} = -r_2/K_2$. It follows that the coexistence of the two population can happen only under the restriction

$$p_1 p_2 < 1, \quad \frac{r_1}{r_2} > p_2, \quad \frac{r_2}{r_1} > p_1,$$

and similar conditions appear for any of the other fixed points. We summarize this parameter dependence of fixed points, in Fig. 8, where without loss of generality we have



Fig. 8 Outcomes of the model for a single community and two populations when $r_1 > r_2$ and on the parameter space $p_1 = -\lambda_{21}K_1/r_1 v/s p_2 = -\lambda_{12}K_2/r_2$. Long-term behavior on each zone: (a) coexistence, (b) species 1 wins, (c) species 2 wins and (d) strong competition. Points 1 and 3 are the coordinates for the analyzes carried out in "Coexistence and the competition/colonization trade-off" and "Effect of the metacommunity spatial structure" and Appendix 3, respectively

assumed that $r_1 \ge r_2$. Long-term behavior correspond to the classical Lotka-Volterra competition: a) coexistence, b) species 1 wins, c) species 2 wins, and d) strong competition (where the species with the largest initial biomass wins), that correspond to each of the zones in Fig. 8. The conditions for each scenario are:

- (a) $p_1 < r_2/r_1$ and $p_2 < r_1/r_2$. Since in this case $p_1p_2 < 1$, coexistence of species is expected.
- (b) $p_1 > r_2/r_1$ and $p_2 < r_1/r_2$. It follows that species 1 kicks in and at large times it is expected to converge asymptotically towards $(-r_1/\alpha_{11}, 0) = (K_1, 0)$.
- (c) $p_1 < r_2/r_1$ and $p_2 > r_1/r_2$. Species 2 dominates and the solution is expected to converge asymptotically towards $(0, -r_2/\alpha_{22}, 0) = (0, K_2)$. Moreover, since $p_1 < r_2/r_1$ and $p_1p_2 > 1$ we get that

$$\bar{x}_1 = \frac{-r_1\alpha_{22} + r_2\alpha_{12}}{\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}} = \frac{1}{\alpha_{11}} \frac{r_2p_2 - r_1}{1 - p_1p_2} > 0,$$

and

$$\bar{x}_2 = \frac{-r_2\alpha_{11} + r_1\alpha_{21}}{\alpha_{11}\alpha_{22} - \alpha_{12}\alpha_{21}} = \frac{1}{\alpha_{22}}\frac{r_1p_1 - r_2}{1 - p_1p_2} < 0$$

i.e., the second coordinate of the coexistence scenario vanishes and

d) $p_1 > r_2/r_1$ and $p_2 > r_1/r_2$. In this last zone conditions imply that both winner-takes-all scenario

are possible, and that the coexistence fixed point (\bar{x}_1, \bar{x}_2) exists but it is unstable. Therefore, according to initial condition, we expect to converge at large times towards either $(0, K_2)$ or $(K_1, 0)$.

Appendix 3. Additional results for two species competition with priority effects

Results for the dynamics of two species in a central community within a metacommunity architecture with three local communities

For each pair (b_1, b_2) with b_i taking values from 0.1 to 0.9 with incremental step 0.1, we performed 150 simulations. We report the empirical average of biomass of both species on the central community.

The results of the model are shown in the upper subplots of Fig. 9. One observes that the species with larger dispersal

rates dominates the long-term solutions in the central community. In the bottom panel of Fig. 9 we plot the probability that species 1 wins as a function of the difference $b_1 - b_2$. We find a shape very similar to the ones described in literature (see, e.g., Calcagno et al. 2006).

Results for two species competition under priority effects in a metacommunity with two local communities

The first case is a symmetrical one, in which the outcome is the expected one for the classical Lotka-Volterra model (i.e., for each community, the species with the larger initial biomass will win). In our example, species 1 wins in community 2 due to its larger initial biomass condition and species 2 wins in community 2 for analogous reasons (Fig. 10 upper panel). Here, species 1 cannot disperse and species 2 dispersal rate b_2 is low. In the second scenario, a small increase in b_2 and no dispersal of species 1, will

Fig. 9 Simulations made for parameters $r_1 = r_2 = 2$, $K_{i1} = K_{i2} = 10$ (for all i = 1, 2, 3). All ε_{ij} are 0 except for $\varepsilon_{21} = \varepsilon_{23} = -\varepsilon_{11} = -\varepsilon_{33} =$ 0.1 and $\lambda_{21} = \lambda_{12} = -0.21$. (top) We show the empirical mean calculated for species 1 and 2 in a central community under a strong competition scenario where species with higher initial biomass will win according to the classical Lotka-Volterra model of competition without stochastic dispersal. (down) We show the probability that species 1 wins as a function of the difference between colonization rates $b_1 - b_2$. As expected, under a symmetric dynamics the species with larger b_i dominates at long times. Dots represents the empirical mean of 150 simulations of the model, for the three-community architecture where the dispersion parameter of species 1 varies. The solid line corresponds to a nonlinear statistical fit



reverse the competence in community 1, and species 2 will win in both communities (Fig. 10, middle panels). And in the third scenario, species 1 only lives in community 1, and a stronger dispersal intensity of species 2 and no dispersal of species 1, will cause coexistence in community 1 (Fig. 10, bottom panel). This last outcome is due to the rapid and massive exchange of biomass of species 2 from one community to another, which can maintain its biomass levels in both communities, specifically causing in community 1 that the biomass condition for winning frequently changes: sometimes species 1 locally dominates due to a temporary larger biomass and sometimes species 2 locally dominates due to the same reason. In Fig. 11 we can visualize the final outcome of the dynamics of both species in community 1 and under each scenario, through the slope (in the long term) of the graph $log(X_{ij}(t))$ vs *t*, which corresponds to the (estimated) Lyapunov exponent.



Fig. 10 Here we show the biomass dynamics of two species in two communities under a priority effect scenario whereby the species that wins in competition is the one with higher initial biomass. The three panels represents three cases of the dynamics of the two species in the two communities, where the dispersal parameter of the inferior competitor species (the one with the lowest initial biomass) varies in each of these columns. The simulations where made over a mean of 50 trajectories and we considered the common parameters $r_1 = 1.6$, $r_2 = 1$, $K_{i1} = 12$, $K_{i2} = 10$ (for all i = 1.2), $\varepsilon_{12} = \varepsilon_{21} = -\varepsilon_{11} = -\varepsilon_{22} = 0.5$, $\lambda_{12} = -0.168$ and $\lambda_{21} = -0.0875$ in (8) for the three cases, with

initial conditions given by $X_{11}(0) = 10$, $X_{12}(0) = 1$, $X_{21}(0) = 1$ and $X_{22}(0) = 10$. The first case is one where the dispersal rate of species 2 is low, $b_2 = 0.003$, and no dispersal of species 1. In the second case we consider only a small increase in the dispersal rate of species 2 ($b_2 = 0.05$). Notice that this subtle change makes this species to increase in biomass in community 1 reversing the priority effect. Finally, in the third case, in local community 2 only species 2 exists but as we increase its dispersal rate ($b_2 = 1$) the priority effect coexistence in local community 1 is now possible

Fig. 11 Convergence of Lyapunov exponents of species 1 and species 2 in community 1 for the corresponding cases of Fig. 10, from top to bottom. In continuous line is depicted one typical trajectory and in dashed line the mean of 50 trajectories, where we can see a softened version of $\log(X_{ij}(t))$ vs t. The slopes of the long-term tendencies tell us the destination of the species: slope ≈ 0 will mean persistence and negative slope indicates extinction



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