Coexistence in metacommunities: A tree-species model

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Abstract

Simple patch-occupancy models of competitive metacommunities have shown that coexistence is possible as long as there is a competition–colonization tradeoff such as that of superior competitors and dispersers. In this paper, we present a model of competition between three species in a dynamic landscape, where patches are being created and destroyed at a different rate. In our model, species interact according to a linear non-transitive hierarchy, such that species Y_3 outcompetes and can invade patches occupied by species Y_2 and this species in turn can outcompete and invade patches occupied by the inferior competitor Y_1. In this hierarchy, inferior competitors cannot invade patches of species with higher competitive ability. Analytical results show that there are regions in the parameter space where coexistence can occur, as well as regions where each of the species exists in isolation depending on species' life-history traits associated with their colonization abilities and extinction proneness as well as with the dynamics of habitat patches. In our model, the condition for coexistence depends explicitly on patch dynamics, which in turn modulate the limiting similarity for species coexistence. Coexistence in metacommunities inhabiting dynamic landscapes although possible is harder to attain than in static ones.

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0. Introduction

One of the fundamental characteristics of ecological systems is that they are spatially heterogeneous, which renders space as an important axis of ecological enquiry (e.g. [45]). Ecologists interested in the role of space envision populations as open systems, not independent from nearby populations with which they interact through the exchange of individuals. This ensemble of interacting populations is what is called a metapopulation or 'population of populations' as presented by Richard Levins in two foundational papers [23,24]. Under the metapopulation paradigm, in addition to the importance of local populations, there is an added emphasis on the dynamics of the ensemble of local populations and the way they interact through migration. Many species exist as metapopulations, and more are expected to do so, considering that the distribution of habitats within landscapes is becoming increasingly patchy through habitat loss, degradation, and fragmentation (see examples in [27,14,13]). Particularly this latter process, fragmentation, is the largest and one of the most important of the many interacting components of global change affecting ecological systems [47] and one of the main causes of species extinction. Landscapes subjected to change through fragmentation represent one of the real world situations where metapopulation theory and models have been shown to be particularly suited to understand species persistence and population dynamics. The process of habitat fragmentation entails the creation of discrete habitat patches whose effect is that local populations interact with each other through the exchange of dispersing individuals, thus behaving as a metapopulation system [15].

The first metapopulation model was proposed by Levins [23,24]. This model assumes a set of identical habitat patches with local populations going extinct and the empty patches being recolonized from the currently occupied ones. This model, of the patch-occupancy type, has proven to be a simple and fruit-full way to understand the basic dynamical properties of metapopulations. This success is reflected in its many subsequent modifications and applications to describe single-species metapopulations (e.g. [11,12,7]), two-species (e.g. [18,37,10,30,31]), and multi-species interactions in metacommunities (e.g., [44,17,21,30]). All these models assume that patches are not only identical, but also static. This latter assumption means that patches are neither created nor destroyed or that their dynamics is so slow that does not affect the dynamics of the populations inhabiting them. However, as mentioned above, the undergoing fragmentation of habitats all across the globe and their effect on species extinction means that patches are being created and destroyed at different rates and that this matters for species persistence. Following the lead of Lande [22], Nee and May ([30], N&M hereafter) proposed a general model designed to understand the effect of habitat destruction (characterized as a fraction of habitat unavailable for colonization) upon species interaction and persistence in patchy landscapes. The scenario modeled by N&M consists of two competing species utilizing resources in the same habitat patches. N&M demonstrated that habitat destruction might have counter-intuitive consequences: favoring coexistence of both types, or the extinction of the superior competitor, thus favoring the persistence of the inferior competitor when it is better at colonizing empty patches (a weedy strategy). The simplicity and generality of this result has prompted its application to multi-species

communities or metacommunities, under the assumption of an explicit competitive hierarchy and the existence of a tradeoff between competition and colonization abilities [44,43,45,40] and has fostered the development of spatially explicit models where the spatial pattern and rate of habitat destruction have been shown to have an effect upon species interaction and persistence [6,29,48,3,19,43,20].

In addition, even if fragmentation were not a problem, the fact that habitat patches are made of living entities, such as shrubs, trees or single individuals, that recruit, grow, and eventually die, means that patch dynamics is relevant to understand metapopulation dynamics [26,33,20,1]. In this paper, our aim is to understand species coexistence in dynamic landscapes. Previous studies of interspecific competition in a metapopulation context have made use of a simple competitive hierarchy to model the effect of species upon each other [25,44]. However, these models assume that the habitat is fixed (i.e., there is no creation nor destruction of patches) and that inferior competitors are invisible for superior competitors so that the latter do not distinguish between empty patches and patches occupied by competitively inferior species. For these models, it has been shown that coexistence is possible as long as there is a competition–colonization tradeoff such that superior competitors are per dispersers. However, it has not yet been explored if this condition holds for metapopulations in dynamic landscapes. In this paper, we present a model to assess the effect of patch dynamics upon coexistence in a competitive metacommunity. We use the two-species model proposed by Mena-Lorca et al. [28] as our point of departure. However, in this case we consider three species Y_1, Y_2, Y_3, whose patch competitive abilities form a hierarchical linear order, such that $Y_1 < Y_2 < Y_3$, which implies that the competitively superior species can colonize empty patches and also displace competitively inferior species from already occupied ones. In our model patches have dynamics of their own, being created and destroyed at different rates. Our interest is in identifying the condition that allows for species coexistence and how it is affected by patch dynamics. We show that species coexistence in dynamic landscapes depends upon species life-history attributes as well as upon landscape characteristics, which jointly define a limiting similarity criterion for coexistence.

1. Mathematical model

Metapopulation models share important similarities to infectious disease models (e.g. [9,26,31,28]) such that the latter only require minor modifications to describe the dynamics of a whole variety of ecological systems [5]. Similar to some epidemiological models that incorporate among hosts differences in susceptibility to a disease, metapopulations models can be made more realistic by incorporating differences in patch quality [26,20,16]. Patch quality in the model developed here is associated with higher or lower extinction rate of patches (i.e. patch mortality rates) due to density-dependent effects. This definition of patch quality is derived from epidemiology and underscore the fact that patches are usually other organisms, such as individual plants or animals or groups of individuals conforming a structure such as forests patches. Thus, not only infectious diseases can impose dynamics in the host (patch) population. Organisms that colonize others require, depending upon time and spatial scale considerations, that models incorporate patch dynamics to better describe the evolving nature of the interaction between organisms and the patches they inhabit, whereas Hastings (2003) claims quality changes. Although most

metapopulation models have assumed that patches are objects without dynamics, or whose dynamics is too slow to be relevant for the organisms inhabiting them, recent theoretical (e.g. [20,16]) and empirical evidences (e.g. [4,46,36,38,39]) have pointed out that patch demography and dynamics do affect metapopulation persistence and patterns in metacommunities [35].

Our model envisions a landscape wherein habitat patches are dynamic, that is they are created and destroyed. The number of habitat patches N available for colonization is created at a per patch rate b and they are destroyed in a density-dependent fashion. We assume that the dynamics of the habitat patches is of logistic type of the form

$$\dot{N} = bN - \theta(N),$$

where $\theta(N) = N(e + \frac{r}{K}N)$, with K representing the total maximum allowable number of patches in the system, $\frac{N}{K}$ being the fraction of suitable patches [8] and $r = b - e$ is the net growth rate since b is the per patch rate of creation of new empty patches and e is the per patch destruction rate of patches. Using a logistic type dynamics is justified in that we are dealing with biotic patches (e.g., plants and corals that are generated and die according to a demographic process. Species Y_1, Y_2, Y_3 occupy the empty habitat patches but are excluded from patches colonized by species that are competitively superior. The competitive hierarchy follows a linear order of the form $Y_1 < Y_2 < Y_3$. Thus, in this model patches can be in four different states, denoted as follows:

V: the number of empty patches
Y_i: the number of patches inhabited by species number i, $i = 1, 2, 3$

Therefore, the total number of patches is $N = V + Y_1 + Y_2 + Y_3$. The patches being created are initially empty and can be colonized by one of the three species at a rate $C_i \frac{Y_i}{N}$, $i = 1, 2, 3$, where C_i represents the maximal patch colonization rate of species i. Because the habitat has a density-dependent extinction rate $\theta(N)$, the rate of extinction corresponding to empty patches is $\theta(N)\frac{V}{N}$ and hence the rate equation for empty patches is

$$\frac{dV}{dt} = bN - C_1 V \frac{Y_1}{N} - C_2 V \frac{Y_2}{N} - C_3 V \frac{Y_3}{N} - \theta(N)\frac{V}{N}.$$

We further consider that occupied patches become extinct at a rate v_i, in addition to their background density-dependent extinction rate. This effect can be thought of as the negative effect of the species upon their habitat patches, as for example when the habitat is also a food resource as in host-parasite systems. Since species are aligned in a hierarchical way, the stronger competitor, species j, will instantaneously outcompete and successfully invade all patches where the weaker species i is present at a rate $a_{ij} C_j \frac{Y_i}{N}$; thus, we do not allow for multiple occupation of patches (see [37,41]). In the above expression, the parameter a_{ij} can be interpreted as an index of habitat affinity, such that

If $a_{ij} > 1$, the presence of the weaker species i facilitates the colonization of the species j, in comparison to the capacity of colonizing the empty patches. In this case, Y_i patches become more attractive for the superior competitor.
If $a_{ij} < 1$, it is easier for the stronger species j to colonize empty patches than the ones occupied by species i.

If $a_{ij} = 1$, the colonization of the species j to the patches either occupied by species i or empty occurs at the same rate.

In this model, we assume that the patches Y_j are neither invaded nor colonized by a species i; thus, the equations for Y_1, Y_2, Y_3, are

$$
\begin{aligned}
\dot{V} &= bN - C_1 V \frac{Y_1}{N} - C_2 V \frac{Y_2}{N} - C_3 V \frac{Y_3}{N} - \theta(N) \frac{V}{N} \\
\dot{Y}_1 &= C_1 V \frac{Y_1}{N} - a_{12} C_2 Y_1 \frac{Y_2}{N} - a_{13} C_3 Y_1 \frac{Y_3}{N} - v_1 Y_1 - \theta(N) \frac{Y_1}{N} \\
\dot{Y}_2 &= C_2 V \frac{Y_2}{N} - a_{23} C_3 Y_2 \frac{Y_3}{N} + a_{12} C_2 Y_1 \frac{Y_2}{N} - v_2 Y_2 - \theta(N) \frac{Y_2}{N} \\
\dot{Y}_3 &= C_3 V \frac{Y_3}{N} + a_{23} C_3 Y_2 \frac{Y_3}{N} + a_{13} C_3 Y_1 \frac{Y_3}{N} - v_3 Y_3 - \theta(N) \frac{Y_3}{N}.
\end{aligned}
\tag{1}
$$

Thus, by adding up the preceding equations, we may have the equation for N:

$$
\frac{\mathrm{d}N}{\mathrm{d}t} = rN \left(1 - \frac{N}{K} \right) - v_1 Y_1 - v_2 Y_2 - v_3 Y_3.
\tag{2}
$$

Note that the model formed by Eqs. (1) and (2) is well posed; firstly, we have to take into account that because $N = V + Y_1 + Y_2 + Y_3$, the system has, in fact, four variables, so it suffices to analyze system (1), and the region we are interested in is the compact

$$
\mathbb{K} = \{ (V, Y_1, Y_2, Y_3) : \ V + Y_1 + Y_2 + Y_3 \leqslant K; \ V, Y_1, Y_2, Y_3 \geqslant 0 \}.
$$

This system is positively invariant in $\mathbb{K}$, since

$$
V = 0 \ \text{implies} \ \frac{\mathrm{d}V}{\mathrm{d}t} = bN,
$$

thus, $V(t) \geqslant 0$, $\forall t \geqslant 0$.

On the other hand, by using the equations in (1), we get that if $Y_i = 0$, then $\frac{\mathrm{d}Y_i}{\mathrm{d}t} = 0$, which in turn says that the planes $Y_i = 0$ are an invariant set for the system. Therefore, the solutions of the system for initial values in $\mathbb{R}_{0+}^4$ remain inside $\mathbb{R}_{0+}^4$. Now, by using Eq. (2), we see that $V + Y_1 + Y_2 + Y_3 \leqslant K$. All of the preceding considerations guarantee that the solutions will always have positive or null components, and their sum will not exceed the capacity of the habitat.

To simplify the system formed by Eqs. (1) and (2), we define the following variables:

$$
I_1 = \frac{Y_1}{N} \quad I_2 = \frac{Y_2}{N} \quad I_3 = \frac{Y_3}{N} \quad I_0 = \frac{V}{N}.
$$

With these new variables, our system (1) and (2) reduces to the four-variable system (I_1, I_2, I_3, N), as follows:

For each i, $i = 1, 2, 3$,

$$
\frac{\mathrm{d}I_i}{\mathrm{d}t} = \frac{\frac{\mathrm{d}Y_i}{\mathrm{d}t}}{N} - \frac{Y_i}{N} \frac{\frac{\mathrm{d}N}{\mathrm{d}t}}{N}.
$$

Since

$$\frac{\frac{dN}{dt}}{N} = r\left(1 - \frac{N}{K}\right) - v_1 I_1 - v_2 I_2 - v_3 I_3$$

and

$$\frac{\frac{dY_1}{dt}}{N} = C_1 I_0 I_1 - a_{12} C_2 I_1 I_2 - a_{13} C_3 I_1 I_3 - v_1 I_1 - \left(e + \frac{r}{K} N\right) I_1,$$

thus we get, for the first species, the equation:

$$\frac{dI_1}{dt} = I_1(C_1 I_0 - a_{12} C_2 I_2 - a_{13} C_3 I_3 - v_1 - e - r + v_1 I_1 + v_2 I_2 + v_3 I_3).$$

Now, since

$$I_0 = 1 - (I_1 + I_2 + I_3),$$

we have

$$\frac{dI_1}{dt} = I_1\{I_1(C_1 + v_1) + I_2(-C_2 a_{12} + v_2 - C_1) - I_3(-v_3 + a_{13} C_3 + C_1) + C_1 - v_1 - e - r\}$$

in an analogous fashion; we have the equations for $\frac{dI_2}{dt}$ and $\frac{dI_3}{dt}$.

To further simplify the analysis, we re-scale time according to the dynamics of the patches, which is given by r. Thus

$$t = \tau/r \text{ con } \tau > 0.$$

Similarly, we define

$$c_i = \frac{C_i}{r} \quad e_i = \frac{v_i}{r},$$
$$e_0 = \frac{e}{r} \quad h = \frac{N}{K},$$

where h represents the fraction of suitable patches in the system [8]. The preceding operation allows us to re-scale the system under analysis in terms of the dynamics of the patches where it is embedded, thus linking explicitly metapopulation dynamics and patch dynamics. One may reduce the system even more. The first equation, for example, reduces to

$$\frac{dI_1}{d\tau} = \left[(-c_1 + e_1)I_1 + (-c_1 - a_{12}c_2 + e_2)I_2 + (-c_1 - a_{13}c_3 + e_3)I_3 - e_1 - \frac{b}{r} + c_1\right]I_1.$$

Since

$$r = b - e \iff \frac{b}{r} = 1 + e_0,$$

by replacing the last expression $\frac{dI_1}{d\tau}$, we get

$$\frac{dI_1}{d\tau} = [(-c_1 + e_1)I_1 + (-c_1 - a_{12}c_2 + e_2)I_2 + (-c_1 - a_{13}c_3 + e_3)I_3 - e_1 - 1 - e_0 + c_1]I_1.$$

In a completely analogous way, we obtain the other equations that form the following system:

$$\frac{dI_1}{d\tau} = [(-c_1 + e_1)I_1 + (-c_1 - a_{12}c_2 + e_2)I_2 + (-c_1 - a_{13}c_3 + e_3)I_3 - e_1 - 1 - e_0 + c_1]I_1$$

$$\frac{dI_2}{d\tau} = [(-c_2 + a_{12}c_2 + e_1)I_1 + (-c_2 + e_2)I_2 + (-c_2 - a_{23}c_3 + e_3)I_3 - e_2 - 1 - e_0 + c_2]I_2$$

$$\frac{dI_3}{d\tau} = [(-c_3 + a_{13}c_3 + e_1)I_1 + (-c_3 + a_{23}c_3 + e_2)I_2 + (-c_3 + e_3)I_3 - e_3 - 1 - e_0 + c_3]I_3 \qquad (3)$$

$$\frac{dh}{d\tau} = (1 - h - e_1I_1 - e_2I_2 - e_3I_3)h.$$

From now on, we will work with this system in the compact region

$$K = \{(I_1, I_2, I_3, h) \in \mathbb{R}^4 : I_1, I_2, I_3, h \geqslant 0, \ I_1 + I_2 + I_3 \leqslant 1; \ h \leqslant 1\},$$

where K is positively invariant since each plane $I_i = 0$, $i = 1,2,3$ and $h = 0$ is invariant and

$$\left.\frac{d(I_1 + I_2 + I_3)}{d\tau}\right|_{I_1+I_2+I_3=1} = -e_0 - h < 0$$

and $\frac{dh}{d\tau}$ at $h = 1$ is negative.

Notice that the first three equations in (3) depend only on I_1, I_2, I_3 and do not depend on h.

2. Equilibrium points

The equilibrium points are the solutions of the algebraic system

$$[(-c_1 + e_1)I_1 + (-c_1 - a_{12}c_2 + e_2)I_2 + (-c_1 - a_{13}c_3 + e_3)I_3 - e_1 - 1 - e_0 + c_1]I_1 = 0$$

$$[(-c_2 + a_{12}c_2 + e_1)I_1 + (-c_2 + e_2)I_2 + (-c_2 - a_{23}c_3 + e_3)I_3 - e_2 - 1 - e_0 + c_2]I_2 = 0$$

$$[(-c_3 + a_{13}c_3 + e_1)I_1 + (-c_3 + a_{23}c_3 + e_2)I_2 + (-c_3 + e_3)I_3 - e_3 - 1 - e_0 + c_3]I_3 = 0 \qquad (4)$$

$$(1 - h - e_1I_1 - e_2I_2 - e_3I_3)h = 0.$$

We will denote the equilibrium point as $E = (I_1, I_2, I_3, h)$. The trivial equilibrium point is $E_{0000} = (0,0,0,0)$; the equilibrium point for the empty habitat is $E_{0001} = (0,0,0,1)$. Note that in (4) the first three equations are independent of the last one. Now, if $h \neq 0$, by using the last equation in (4), we get

$$h = 1 - e_1I_1 - e_2I_2 - e_3I_3 \qquad (5)$$

and hence, to get the other equilibrium points it suffices to find their first three coordinates (by using only the first three equations in (4)) and substituting these into (5) to find the fourth coordinate of the equilibrium point. Note also that, for each $P = (I_1, I_2, I_3)$, there are two equilibria that differ only in their fourth coordinate, that is, $E = (P, 0) = (a, b, c, 0)$ and $E = (P, h) = (a, b, c, 1 - e_1a - e_2b - e_3b)$.

These points may be classified into two groups, those corresponding to $h = 0$ or $h > 0$. Although the equilibrium points with $h = 0$ are not biologically meaningful (since they imply that there is no suitable habitat), their significance, which will become apparent once we know their stability, resides in how this point is approached.

2.1. Existence of only one species

If $I_i = I_j = 0$ and $I_k > 0$, with $i,j,k \in \{1,2,3\}$, $i,j \neq k$ we have that

$$I_k^* = 1 - \frac{1 + e_0}{c_k - e_k}.$$

Now, if we define $\mathscr{R}_k = \frac{c_k}{1 + e_0 + e_k}$, we have that

$$I_k^* = \frac{(e_k + 1 + e_0)(\mathscr{R}_k - 1)}{c_k - e_k}.$$

Note that $\mathscr{R}_k \geqslant 1$ implies $c_k \geqslant e_k$, and since $I_k^* = 1 - \frac{1 + e_0}{c_k - e_k}$, we have that $\mathscr{R}_k \geqslant 1$ which implies that $0 \leqslant I_k^* \leqslant 1$. Thus, $\mathscr{R}_k$ is the *basic reproductive number* of theoretical epidemiology [2]. However, note that in this case $\mathscr{R}_k$ is not only a function of the life history of the species as in classical Levin type metapopulation models, which is given by its colonization and extinction rates [26,8], but it is also affected by the dynamics of the patches (see [20]). Because the quantity $\frac{1}{1 + e_0 + e_k}$ can be interpreted as the average lifetime of patch k, $\mathscr{R}_k$ is equivalent to the average number of new colonizations produced by a patch in state k during its lifetime. Then, it becomes obvious that if $\mathscr{R}_k > 1$ empty patches will be colonized and the species will attain a positive equilibrium. Thus, the non-trivial equilibrium points corresponding to each species in isolation are feasible if and only if their basic reproductive number is greater than or equal to one, and they are $E_{1001} = (I_1^*, 0, 0, 1 - e_1 I_1^*)$, $E_{0101} = (0, I_2^*, 0, 1 - e_2 I_2^*)$, $E_{0011} = (0, 0, I_3^*, 1 - e_3 I_3^*)$, $E_{1000} = (I_1^*, 0, 0, 0)$, $E_{0100} = (0, I_2^*, 0, 0)$, $E_{0010} = (0, 0, I_3^*, 0)$.

2.2. Two-species coexistence

If $I_k = 0$, with $k \neq i,j$, $i < j$, $I_i \neq 0 \neq I_j$, we define

$$\Psi_{ij}^c(a_{ij}) = a_{ij}c_j + c_i - c_j,$$

$$\Psi_{ij}^e(a_{ij}) = a_{ij}c_j + e_i - e_j,$$

where $\Psi_{ij}^c(a_{ij})$ represents the net flux of empty patches that become patches j through i, discounted by the direct colonizations of empty patches by the superior competitor j. This is a measure of the relative importance of the indirect path, which is a reflection of the species' competitive ability. Similarly, $\Psi_{ij}^e(a_{ij})$ represents the net flux of patches that are lost from i once direct losses from j are discounted. In short, these terms represent the importance of the path $a_{ij}c_j$ (or competition path) in comparison with the direct colonization or extinction paths. Note that, in a single-species case, the quotient $\frac{\Psi_{ij}^c(a_{ij})}{\Psi_{ij}^e(a_{ij})}$ is equivalent to Levin's basic reproductive number $\frac{c}{e}$. However, in the present case it can be interpreted as a measure of the importance of the competitive path to the reproductive number of the dominant species.

Let

$$P_{110} = \left(\frac{1 + e_0}{\Psi_{12}^e(a_{12})} + \frac{e_2 - c_2}{\Psi_{12}^c(a_{12})}, \frac{-(1 + e_0)}{\Psi_{12}^e(a_{12})} + \frac{c_1 - e_1}{\Psi_{12}^c(a_{12})}, 0 \right),$$

then $E_{1101} = (P, h)$ and $E_{1100} = (P, 0)$ are the equilibrium points in the absence of the strongest competitor (species 3). In a completely analogous way as done in Mena-Lorca et al. [28], we

use P_{101}, P_{011} to obtain the equilibrium points E_{1011} and E_{0111}. In summary, solutions (5) give a total of 16 feasible equilibrium points with coordinates (I_1, I_2, I_3, h).

2.3. Conditions for two-species coexistence

In this section, we will use species 1 and 2 without loss of generality, to represent typical one to one species interaction. Due to the symmetry in our model equations, results for this case are analogous to the cases for species 1, 3 and 2, 3. We will now consider the equilibrium points of biological importance.

Given that we handle now a two-species model, we will simplify the notation by relabeling $\Psi_{12}^c(a_{12}) = \Psi_1(a)$ and $\Psi_{12}^e(a_{12}) = \Psi_2(a)$ defined as

$$\Psi_1(a) = ac_2 - (c_2 - c_1),$$
$$\Psi_2(a) = ac_2 - (e_2 - e_1).$$

Hence, the equilibrium points where coexistence of both species is possible are

$$E_{1100} = \left(\frac{1 + e_0}{\Psi_2} + \frac{e_2 - c_2}{\Psi_1}, \frac{-(1 + e_0)}{\Psi_2} + \frac{c_1 - e_1}{\Psi_1}, 0, 0 \right),$$
$$E_{1101} = \left(\frac{(1 + e_0)}{\Psi_2} + \frac{e_2 - c_2}{\Psi_1}, \frac{-(1 + e_0)}{\Psi_2} + \frac{c_1 - e_1}{\Psi_1}, 0, h^* \right),$$

where $h^* = 1 - e_1 I_1^{*12} - e_2 I_2^{*12}$ and I_1^{*12}, I_2^{*12} represent the first and the second components of E_{1100}, respectively. With this change in notation, we can refer directly to Mena-Lorca et al. [28] when needed.

Note that the first and the second coordinates of E_{1100} and E_{1101} must be positive, and this holds if

$$\frac{e_2}{\Psi_1}\left(\frac{c_2}{e_2} - 1\right) < \frac{1 + e_0}{\Psi_2} < \frac{e_1}{\Psi_1}\left(\frac{c_1}{e_1} - 1\right). \tag{6}$$

As the reader can see, this is a relation between reproductive numbers; the term in the middle corresponds, in the original parameters, to $b/(aC_2 - v_2 + v_1)$. So, since b is the gross rate of creation of empty habitat, as b increases, the difference in the reproductive numbers of species that allows their coexistence also increases. For example if b is large, then the term $\frac{1+e_0}{\Psi_2}$ is large too, and the inferior competitor has to colonize empty patches at a higher rate to compensate the extra growth of the superior competitor. This competitor can colonize both empty patches and patches colonized by the inferior competitor and therefore it would occupy a larger proportion of the habitat very quickly. This process forces the inferior competitor to increase its colonization ability in order to avoid competitive exclusion by the superior one. On the other hand if b is small, the term $\frac{1+e_0}{\Psi_2}$ is also small and the inferior competitor can afford to be less efficient in colonization ability since the abundance of the superior competitor is limited by the rate of habitat production. The term $\frac{1+e_0}{\Psi_2}$ then sets a limiting similarity in colonization abilities (see also [44,21]), which depends both on the attributes of the species and the landscape wherein it is embedded. To finish this discussion, note that if both reproductive numbers are equal to one, coexistence is not possible, and the superior competitor wins.

We define, following Mena-Lorca et al. [28],

$$f(a) = \frac{\Psi_1(a)}{\Psi_2(a)} = \frac{a - a_c}{a - a_e},$$

which can be interpreted as the relative contribution of the competitive path to the reproductive number of the dominant species or, alternatively, as the proportion of patches that a dominant competitor will occupy if introduced in a population of patches occupied by the subdominant species, where

$$a_c = \frac{c_2 - c_1}{c_2},$$

$$a_e = \frac{e_2 - e_1}{c_2}.$$

Lemma 1

(a) *If $a_c < a_e$, then E_{1100} and E_{1101} exist if and only if*

$$a \in f^{-1}\left(\frac{c_2 - e_2}{1 + e_0}, \frac{c_1 - e_1}{1 + e_0}\right) \quad \text{and} \quad a > a_c. \tag{7}$$

(b) *If $a_e < a_c$, then E_{1100} and E_{1101} exist if and only if*

$$a \in f^{-1}\left(\frac{c_1 - e_1}{1 + e_0}, \frac{c_2 - e_2}{1 + e_0}\right) \quad \text{and} \quad a < a_c. \tag{8}$$

(c) E_{1000} *and* E_{1001} *exist if and only if* $\mathcal{R}_1 > 1$.
(d) E_{0100} *and* E_{0101} *exist if and only if* $\mathcal{R}_2 > 1$.

3. Stability of equilibrium points

Mathematically, the study of a two-species system is equivalent to the study of (3) on the plane $I_3 = 0$, for example. On that plane, the system is invariant as are the other two systems obtained by setting $I_i = 0$ and $h = 0$. Let K_3 be the set

$$K_3 = \{(I_1, I_2, I_3, h) \in \mathbb{R}^4 : I_3 = 0, I_1, I_2, h \geqslant 0, \ I_1 + I_2 \leqslant 1; \ h \leqslant 1\},$$

and similarly for K_0, K_1 and K_2. This is the system studied in Mena-Lorca et al. [28] where the following results are proven.

Lemma 2. *Each pair of equilibrium points that differs at most in the third coordinate is connected by a heteroclitic orbit.*

Given the preceding result, the following step is the stability of the equilibrium point E_{1100} in the set K_3 with $h = 0$, which we will denote by K_3^0. For this, we establish the following:

Theorem 3

(1) *If condition (7) and $a_e < a$ hold, then E_{1100} is locally asymptotically stable, and so, it is globally asymptotically stable in K_3^0 deprived the axes I_1 and I_2.*

(2) *If, on the other hand, condition (8) and $a_e > a$ hold, then we have the same result as above.*

Theorem 4

(1) *The equilibrium point E_{1101} is globally asymptotically stable in K_3 provided that E_{1101} is locally asymptotically stable.*

(2) *There are no periodic orbits in K_3 if E_{1101} is locally stable.*

The proof of the stability of E_{1101} is provided in Mena-Lorca et al. [28].

Theorem 5. *Assume that E_{1100} is locally asymptotically stable. Then, E_{1101} is globally stable in the interior of K_3.*

Similarly, (global) stability can be shown for E_{0111}, E_{1011}, restricted to the 3 dimensional invariant manifolds K_1 and K_2, respectively. The next theorem shows that under certain conditions all three species persist in the community in

$$K = \{(I_1, I_2, I_3, h) \in \mathbb{R}^4 : I_1, I_2, I_3, h \geqslant 0, \ I_1 + I_2 + I_3 \leqslant 1; \ h \leqslant 1\}.$$

Theorem 6. *Let* $X_2 = \{(I_1, \ I_2, \ I_3, \ h) \in K : I_1 = 0 \ \text{or} \ I_2 = 0 \ \text{or} \ I_3 = 0\}$, $X_1 = K - X_2$. *If* $\Psi_{ij}^c(a_{ij})$, $\Psi_{ij}^e(a_{ij})$ *have the same sign*, $\mathcal{R}_k > 1$, $k = 1, 2, 3$, $a_{23} \approx 0$ *and* $a_{12} \approx 2 \approx a_{13}$ *and*

$$\frac{(c_j - e_j)}{\Psi_{ij}^c(a_{ij})} < \frac{1 + e_0}{\Psi_{ij}^e(a_{ij})} < \frac{c_i - e_i}{\Psi_{ij}^c(a_{ij})} \quad \text{with} \quad i < j, \ i,j = 1,2,3, \tag{9}$$

then X_2 is a uniform strong repeller for X_1, that is, there is some $\epsilon > 0$ such that

$$\liminf_{t \to \infty} d(\phi_t(x), X_2) > \epsilon, \quad \text{for all } x \in X_1,$$

where ϕ_t is the semiflow of system (3) in X_1.

Proof. The proof is based on Theorem 4.5 in [42, p. 426] and we use his notation. Note that our $X_2 = \bigcup_{j=1}^3 K_j$ and since X_2 is a closed set in a compact set K, X_2 is compact.

Setting $I_j = 0$ in system (3), we get $\frac{\mathrm{d}I_j}{\mathrm{d}\tau} = 0$ for all τ, then each K_j ($j = 1, 2, 3$) is invariant for the flow ϕ. Analogously, if we choose $h = 0, \frac{\mathrm{d}h}{\mathrm{d}\tau} = 0$ for all τ. Therefore,

$$Y_2 = \{x \in X_2 : \phi_t(x) \in X_2, \forall t > 0\} = X_2.$$

Notice that Y_2 could properly contain X_2 but in this case these sets are equal. On the other hand, if we set $h = 1$, we get $\frac{\mathrm{d}h}{\mathrm{d}\tau} < 0$, so K is positively invariant; therefore, X_1 is also forward invariant for the semiflow.

From the results given in Lemma 2 and Theorems 3–5, we know that the omega limit sets $\omega(x)$ for each $x \in X_2$ are contained in X_2 and therefore we have that

$$\Omega_2 = \bigcup_{x \in X_2} \omega(x)$$

is the union of the fourteen equilibrium points E_{ijkl} (with $i,j,k,l \in \{0,1\}$) in X_2.

By analysis of the explicit eigenvalues and eigenvectors for all of the fourteen boundary equilibria, we can claim that these points cannot be connected into a cyclic chain. To prove our claim (and without loss of generality), we will study the case of K_3.

The equilibrium points in K_3 are E_{0000}, E_{0001}, E_{1000}, E_{0100}, E_{1001}, E_{0101}, E_{1100} and E_{1101}, each one having only one eigenvector with third non-zero component. By Theorem 5, E_{1101} is a global attractor in the interior of K_3 (since the corresponding hypotheses are satisfied, for instance, (9) with $i = 1$, $j = 2$), therefore the equilibrium points in K_3 cannot form a cyclic chain (the same occurs with the invariant manifold K_1 and K_2) since this would contradict the globally attracting character of E_{1101}.

Given that, by the previous argument, the 8 equilibrium points cannot be cyclically connected within K_3, they still may connect with all the other 6 equilibria outside K_3. Now, the points E_{1101}, E_{0111} and E_{1011} are global attractors in K_1, K_2 and K_3, respectively. Then the connection must happen through the fourth dimension. However, this one dimensional manifold has a tangent spanned by an eigenvector with positive eigenvalue that does not live in X_2 (therefore points into X_1). However, X_1 is positively invariant and therefore cannot contain points that belong to a cyclic chain since, in that case, one of the equilibrium points should have all corresponding eigenvalues with negative real part which, by hypothesis, cannot be true. Thus X_2 has an acyclic isolated covering.

The following are the set of 'fourth' eigenvalues of each point:

$$G_2^{1101} = G_2^{1100} = (-c_3 + a_{13}c_3 + e_1)I_1^{*12} + (-c_3 + a_{23}c_3 + e_2)I_2^{*12}(\mathscr{R}_3 - 1)(1 + e_0 + e_3)$$
    for the points E_{1100} and E_{1101},
$$G_2^{1011} = G_2^{1010} = (-c_2 + a_{12}c_2 + e_1)I_1^{*13} + (-c_2 - a_{23}c_3 + e_3)I_3^{*13} + (\mathscr{R}_2 - 1)(1 + e_0 + e_2)$$
    for the points E_{1010} and E_{1011},
$$G_2^{0111} = G_2^{0110} = (-c_1 - a_{12}c_2 + e_2)I_2^{*23} + (-c_1 - a_{13}c_3 + e_3)I_3^{*23} + (\mathscr{R}_1 - 1)(1 + e_0 + e_1)$$
    for the points E_{0110} and E_{0111},

and since

$$G_2^{1101} > [e_1 + e_2 - 2c_3 + c_3a_{13} + c_3a_{23}] * \min\{I_1^{*12}, I_2^{*12}\} + (\mathscr{R}_3 - 1)(1 + e_0 + e_3),$$
$$G_2^{1011} > [e_1 + e_3 - 2c_2 + c_2a_{12} - c_3a_{23}] * \min\{I_1^{*13}, I_3^{*13}\} + (\mathscr{R}_2 - 1)(1 + e_0 + e_2),$$
$$G_2^{0111} > [e_1 + e_3 - 2c_2 + c_2a_{12} - c_3a_{23}] * \min\{I_2^{*23}, I_3^{*23}\} + (\mathscr{R}_1 - 1)(1 + e_0 + e_1),$$

and $\mathscr{R}_k > 1$, $k = 1, 2, 3$ and $a_{23} \approx 0$ and $a_{12} \approx 2 \approx a_{13}$, by hypothesis, then the unstable manifold of each and every equilibrium point is contained in X_1; so each part of the covering is a weak repeller. On the basis of Thieme's result, X_2 is a uniform strong repeller for X_1, showing that the three-species coexistence is persistent at the metacommunity level. □

4. Conclusion

As implied by conditions (6) and more generally in (9), the coexistence of competing species in dynamic landscapes, as well as their relative similarity in terms of fecundity and mortality or

colonization and extinction depends as much on the attributes of species as on the dynamics attributes of the landscape wherein they are embedded. Thus, the coexistence of species emerges as a consequence of the interaction between species and the environmental setting that they inhabit. In this sense, it is a relational property. Previous analysis of interspecific competition in metacommunities (e.g. [30,44,43,30]) has neglected the dynamical properties of the patches competed for arriving to the conclusion that coexistence is possible as long as there is a tradeoff between competitive ability and dispersal capability. However, as shown in (9) in dynamic landscapes a competition–colonization tradeoff is not sufficient to assure coexistence because patch dynamics modulate the limiting similarity among competing species. In this paper, we have explored the implications upon the steady-states of variable habitat size. As in previous published results [32], we have found that competitive exclusion and coexistence are outcomes that depend on the relative competitive ability of the species and on the similarity in terms of colonization that the species must possess in order to guarantee coexistence, but modulated by patch dynamics.Variable habitat size introduces a whole range of conditions that determine coexistence. Our results indicate that, at least for the case of patch density-dependence mortality (extinction), coexistence is rather a special outcome of the interaction between competing species, and although coexistence is feasible the conditions are much harder to be satisfied. We point out that the results that we have obtained with the density-dependence function $\theta(N)$ are immediately generalizable to a convex non-decreasing function of N with the properties described by Pugliese [34]. This kind of function allows for the partial decoupling of (3). Thus, our treatment of $\theta(N)$ as a logistic density-dependent term involves no loss of generality. Although it can be questioned that patches do actually undergo density-dependent destruction or mortality, this is a realistic assumption as these models apply both to patches and sites as large as local populations or as small as single individuals [44,43], and in this latter case density-dependence is a realistic assumption and a standard way of modeling theoretical populations.

Acknowledgments

References

[1] P. Amarasekare, H. Possingham, Patch dynamics and metapopulation theory: the case of successional species, J. Theoretic. Biol. 209 (2001) 333.
[2] R.M. Anderson, R.M. May, Infectious Diseases of Humans, Oxford Science Publications, Great Britain, 1991.
[3] J. Bascompte, R.V. Solé, Habitat fragmentation and extinction thresholds in spatially explicit models, J. Anim. Ecol. 65 (1996) 465.
[4] R. Biedermann, Modelling the spatial dynamics and persistence of the leaf beetle *Gonioctena olivacea* in dynamic habitats, Oikos 107 (2004) 645.
[5] A. Dobson, Metalife! Science 301 (2003) 1488.
[6] C. Dytham, Habitat destruction and competitive coexistence: a cellular model, J. Anim. Ecol. 63 (1994) 490.

 [7] N.J. Gotelli, Metapopulation models: the rescue effect, the propagule rain, and the core-satellite hypothesis, Am. Nat. 138 (1991) 768.
 [8] M. Gyllenberg, I. Hanski, A. Hastings, Structured metapopulation models, in: I. Hanski, M.E. Gilpin (Eds.), Metapopulation Biology, Academic Press, San Diego, California, 1997, p. 93.
 [9] B. Grenfell, J. Harwood, (Meta) population dynamics of infectious diseases, Trends Ecol. Evol. 12 (1997) 395.
[10] I. Hanski, Coexistence of competitors in a patchy environment, Ecology 64 (1983) 493.
[11] I. Hanski, Single species spatial dynamics may contribute to long term raity and commoness, Ecology 66 (1985) 335.
[12] I. Hanski, Single species metapopulation dynamics: concepts, models and observation, J. Linn. Soc. 42 (1991) 17.
[13] I. Hanski, Metapopulation Ecology, Oxford University, Oxford, 1999.
[14] I. Hanski, M.E. Gilpin, Metapopulation Biology: Ecology, Genetics and Evolution, Academic Press, San Diego, 1997.
[15] I. Hanski, D. Simberloff, The metapopulation approach, its history, conceptual domain, and application to conservation biology, in: I. Hanski, M.E. Gilpin (Eds.), Metapopulation Biology, Academic Press, San Diego, California, 1997, p. 5.
[16] A. Hastings, Metapopulation persistence with age-dependent disturbance or succession, Science 301 (2003) 1525.
[17] R.D. Holt, From metapopulation dynamics to community structure: some consequences of spatial heterogeneity, in: I. Hanski, M. Gilpin (Eds.), Metapopulation Biology: Ecology, Genetics and Evolution, Academic Press, New York, 1997, p. 149.
[18] H.S. Horn, R.H. MacArthur, Competition among fugitive species in a harlequin environment, Ecology 53 (1972) 749.
[19] T.H. Keitt, D.L. Urban, B.T. Milne, Detecting critical scales in fragmented landscapes, Conserv. Ecol. 1 (1997) 4. Available from: <http://www.consecol.org/Journal/voll/issl/art4>.
[20] J.E. Keymer, P.A. Marquet, J.X. Velasco-Hernández, S.A. Levin, Extinction thresholds and metapopulation persistence in dynamics landscapes, Am. Nat. 156 (2000) 478.
[21] A.P. Kinzig, A. Levin, J. Dushoff, S. Pacala, Limiting similarity, species packing, and system stability for hierarchical competition–colonization models, Am. Nat. 153 (1999) 371.
[22] R. Lande, Extinction thresholds in demographic models of territorial populations, Am. Nat. 130 (1987) 624.
[23] R. Levins, Some demographic and genetic consequences of environmental heterogeneity for biological control, Bull. Entomol. Soc. Am. 15 (1969) 237.
[24] R. Levins, Extinction, Lectures on Mathematics in the Life Sciences, 2, Am. Math. Soc., Providence RI, 1970.
[25] R. Levins, D.C. Culver, Regional coexistence and competition between rare species, Nat. Aca. Sci. (U.S.), Proceedings 68 (1971) 1246.
[26] P.A. Marquet, J.X. Velasco-Hernández, A source-sink patch occupancy metapopulation model, Rev. Chilena Hist. Nat. 70 (1997) 371.
[27] D.R. McCullough, Metapopulations and Wildlife Conservation, Island Press, Washington, 1996.
[28] J. Mena-Lorca, J.X. Velasco-Hernandez, C. Castillo-Chavez, Density-dependent dynamics and superinfection in an epidemic model, IMA J. Math. Appl. Med. Biol. 16 (1999) 307.
[29] A. Moilanen, I. Hanski, Habitat destruction and coexistence of competitors in a spatially realistic metapopulation model, J. Anim. Ecol. 64 (1995) 141.
[30] S. Nee, R.M. May, Dynamics of metapopulations: habitat destruction and competitive coexistence, J. Anim. Ecol. 61 (1992) 37.
[31] S. Nee, R.M. May, M. Hassell, Two species metapopulation models, in: I. Hanski, M. Gilpin (Eds.), Metapopulation Biology: Ecology, Genetics and Evolution, Academic Press, New York, 1997, p. 123.
[32] M.N. Nowak, R.M. May, Superinfection and the evolution of parasite virulence, Proc. R. Soc. Lond. B 255 (1994) 81.
[33] I. Olivieri, D. Covert, P.H. Gouyon, The genetics of transient populations – research at the metapopulations level, Trends Ecol. Evol. 5 (1990) 207.
[34] A. Pugliese, Population models for diseases with no recovery, J. Math. Biol. 28 (1990) 65.
[35] M. Roy, M. Pascual, S.A. Levin, Competitive coexistence in a dynamic landscape, Theoret. Pop. Biol. 66 (2004) 341.

[36] G.R. Schrott, K.A. With, A.T. King, On the importance of landscape history for assessing extinction risk, Ecol. Appl. 15 (2005) 493.

[37] M. Slatkin, Competition and regional coexistence, Ecology 55 (1974) 128.

[38] T. Snall, J. Pennanen, J. Kivisto, L.I. Hanski, Modelling epiphyte metapopulation dynamics in a dynamic forest landscape, Oikos 109 (2005) 209.

[39] T. Snall, J. Ehrlen, H. Rydin, Colonization–extinction dynamics of an epiphyte metapopulation in a dynamic landscape, Ecology 86 (2005) 106.

[40] L. Stone, Biodiversity and habitat destruction: a comparative study of model forest and coral reef ecosystems, Proc. R. Soc. Lond. B 261 (1985) 381.

[41] D.E. Taneyhill, Metapopulation dynamics of multiple species: The geometry of competition in a fragmented habitat, Ecol. Monogr. 70 (2000) 495.

[42] H.R. Thieme, Persistence under relaxed point-dissipativity (with application to an endemic model), SIAM J. Math. Anal. 24 (1993) 407.

[43] D. Tilman, R.M. May, C.L. Lehman, M.A. Nowak, Habitat destruction and the extinction debt, Nature 317 (1994) 65.

[44] D. Tilman, Competition and biodiversity in spatially structured habitats, Ecology 75 (1994) 2.

[45] D. Tilman, P. Kareiva, Spatial Ecology: The Role of Space in Population Dynamics and Interspecific Interactions, Princeton University, Princeton, 1997.

[46] K. Verheyen, M. Vellend, Van Calster, H. Peterken, G. Hermy, Metapopulation dynamics in changing landscapes: a new spatially realistic model for forest plants, Ecology 85 (2004) 3302.

[47] P.M. Vitousek, Beyond global warming: ecology and global change, Ecology 75 (1994) 1861.

[48] K.A. With, T. Crist, Critical thresholds in species' responses to landscape structure, Ecology 76 (1995) 2446.