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Competition and species coexistence in a metapopulation model: can fast asymmetric migration reverse the outcome of competition in a homogeneous environment?

Doanh Nguyen Ngoc [1,2], Rafael Bravo de la Parra[1,3], Miguel A. Zavala[4] and Pierre Auger[1]

[1] UMI UMMISCO 209, IRD, 32 avenue Henri Varagnat, 93143 Bondy cedex, France.

[2] MSI, IFI, 42 Ta Quang Buu street, Hai Ba Trung District, Hanoi, Vietnam.

[3] Departamento de Matemáticas, Universidad de Alcalá, 28871 Alcalá de Henares, Spain.

[4] Departamento de Ecología, Universidad de Alcalá, 28871 Alcalá de Henares, Spain.

Corresponding author: Rafael Bravo de la Parra, E-mail: rafael.bravo@uah.es

Abstract.

We investigate whether asymmetric fast migration can modify the predictions of classical competition theory and, in particular revert species dominance. We consider a model of two species competing for an implicit resource on a habitat divided into two patches. Both patches are connected through constant migration rates and in each patch local dynamics are driven by a Lotka-Volterra competition system.

Local competition is asymmetric with the same superior competitor in both patches. Migration is asymmetric, species dependent and fast in comparison to local competitive interactions. The species and patches are taken to be otherwise similar: in both patches we

assume the same carrying capacities for both species, and the same growth rates and pair-wise competition coefficients for each species.

We show that global dynamics can be described by a classical Lotka-Volterra competition model. We found that by modifying the ratio of intraspecific migration rates for both species all possible combinations of global species relative dominance can be achieved. We find specific conditions for which the local superior competitor is globally excluded. This is to our knowledge the first study showing that fast asymmetric migration can lead to inferior competitor dominance in a homogeneous environment. We conclude that disparity of temporal scales between migration and local dynamics may have important consequences for the maintenance of biodiversity in spatially structured populations.

Keywords

migration-competition trade-off; dominance reversal; time scales; aggregation methods

Introduction

Understanding the mechanisms underlying coexistence in spatially structured habitats (e.g. patchy environments) has been a central goal in theoretical and conservation ecology (Levins 1969, 1970, Levin 1992). One of the most common and simple theoretical explanation for the coexistence of species in mosaic habitats is based on the so called competition-colonization trade-off. According to this mechanism, poorer competitors can stably coexist with competitively superior species by means of their greater colonizing ability. This is, traits linked to colonizing ability such as migration enable fugitive species to capture available sites at faster rate than competitors which favours coexistence in a heterogeneous environment (e.g. Horn & MacArthur 1972; Hasting 1980).

The competition-colonization trade-off is the basis of the Patch Occupancy Metapopulation Theory (POT), a key theoretical framework for exploring population persistence and species coexistence in fragmented landscapes (Hanski, 1999). Applications of

POT have greatly contributed to bridge the gap between theory and field data leading to important contributions in conservation ecology (Hanski and Gilpin 1997). In the last decade, interest in metapopulation biology has rapidly increased covering a range of applications from metapopulation genetics and evolution to landscape ecology or ecosystem ecology. This development has lead to an accumulation of increasing empirical evidence on metapopulation dynamics but has also raised important issues related to the realism of underlying biological assumptions.

As any other theoretical formalization, the POT involves a specific recognition of the temporal scales at which ecological processes operate, with an explicit separation of within patch and among patch dynamics. Specifically, POT focuses on the presence of local populations in habitat patches and it does not include any description of local dynamics. Also, implicit to POT there is the assumption that competition operates at a much faster time scale than colonization-extinction processes. All these assumptions preclude in fact local coexistence and imply that migration cannot influence local competitive interactions. Empirical studies of migration-competition trade-offs, however, have revealed a pattern that is at odds with this assumption, chiefly widespread presence of colonizers species and local coexistence. Amarasekare and Nisbet (2001) have shown that the mismatch between patch occupancy theory and data may arise from the separation of time scales inherent in the patch occupancy framework. Specifically it has been suggested that migration and competition can operate at similar temporal time scales and thus colonizing rates may influence the outcome of local competition.

Mismatches between model assumptions and temporal scales at which ecological phenomena take place, suggest the need to revisit POT underlying assumptions to incorporate a more realistic description of the temporal scales at which key ecological processes operate. Understanding how ecological phenomena interact across temporal scales is indeed a key

need in theoretical ecology (O-Neill et al 1986; Levin 1992). Specifically differences in process time scales may be critical for system dynamical behaviour (Ludwig et al 1978; Lett et al 2005).

In this study we investigate whether explicit consideration of a mismatch of temporal scales between migration and local dynamics can fundamentally challenge the predictions of classical metapopulation theory on species coexistence. Specifically we examine the interplay of local dynamics and migration in a metapopulation for the specific case in which the migration process across patches operates at a faster scale relative to local dynamics. This situation can be found in a range of evolutionary and ecological processes in which gene flow and migration rate due to non sedentary habit can operate at a fast scale relative to selection or population interaction processes. We develop a general model of two species inhabiting two separate patches that are connected through density independent migrations at a fast time scale. Local within-patch competition is assumed to take place at a relatively slower time scale and it is represented by a Lotka-Volterra type competition model.

Previous studies have mainly considered models where they omit disparity of temporal scales between migration and competition; and assume symmetric migrations and heterogeneous environments. For example, Takeuchi (1989) considered symmetric migrations and proved that the corresponding system can be made persistent under appropriate diffusion -symmetric migrations- conditions, even if isolated patches are not persistent, Takeuchi and Lu (1995) extended these results by finding conditions to ensure the permanence and global stability of a positive equilibrium. Permanence indicates that if all species are initially present -even in low abundances- their abundances reach and remain henceforth over a sizeable threshold. Conditions for migration-mediated coexistence are also studied in the case of local communities where the source is explicitly considered, with symmetric migrations for the

competing consumers and no migration for the resource (Abrams and Wilson, 2004; Namba and Hashimoto, 2004) or with also symmetric migrations for the resource (Namba, 2007).

Amarasekare and Nisbet (2001) considered spatial heterogeneity either by allowing for species refuges or by assuming variations in competitive rankings over space such that the superior competitor in some parts of the landscape becomes the inferior competitor in the remnant landscape. So, they establish a source-sink dynamics framework that yields coexistence due to spatial variance in fitness. On the other hand, they also show that under a spatially homogeneous competitive environment –asymmetric competition- differences in migration cannot explain coexistence with the absence of an inferior competitor refuge.

In this study we specifically investigate the life-history trade-off between competitive abilities and migration strategies. Our main result is that fast asymmetric migration can promote dominance of poorer competitor even in a homogeneous environment.

We assume, in contrast with previous studies, that competition is asymmetric, i.e. the same species are the superior and the inferior competitors all across the landscape, and also that migration is asymmetric and occurs on a faster time scale relative to local dynamics. In order to set a homogeneous environment no model parameter, apart from migration rates, is space dependent what allows isolating the relationship between competition abilities and migration strategies.

The proposed model has the form of a four dimensional, two species and two patches, ordinary differential equations system with two time scales. Taking advantage of this last property the system is reduced into a two dimensional system for the total densities of the two species. The form of the reduced system is that of a classical Lotka-Volterra competition model what allows a complete analytical description of the competition outcome in terms of general migration rates and competition intensities.

1. Model structure.

We consider a model with two species competing for an implicit resource on a habitat divided into two patches. Let $n_{ij}(t)$ be the density of species i in patch j at time t with $i, j \in \{1;2\}$.

Both patches are connected through constant migration rates and we suppose that locally, in each patch, there is a Lotka-Volterra competitive dynamics.

Species 1 migrates from patch 1 to patch 2 at a rate $\overline{k}$ and from patch 2 to patch 1 at a rate k. Similarly, the migration rate of species 2 from patch 1 to patch 2 is $\overline{m}$ and from patch 2 to patch 1 is m; so $\overline{k}$, k, $\overline{m}$ and m are constant positive parameters. Migration rates are asymmetric and, in general, different for each species.

We are interested in a life-history trade-off between competitive abilities and migration strategies. We describe such a trade-off in terms of competition coefficients and migration rates.

We assume that local competition is asymmetric with species 1 being the superior competitor in both patches. The species and patches are supposed to be otherwise similar: the same carrying capacity, K, for both species in both patches, the same growth rates for each species in both patches, r_1 for species 1 and r_2 for species 2, and the same pair-wise competition coefficients, a and b, in both patches, measuring the competitive effect of species 2 on species 1 and species 1 on species 2, respectively. To ensure the aforementioned asymmetric competition we assume that $a < 1 < b$.

According to the previous assumptions, the complete model reads as follows:

$$\begin{cases} \dfrac{dn_{11}}{d\tau} = \left(-\bar{k}n_{11} + kn_{12}\right) + \varepsilon r_1 n_{11}\left(1 - \dfrac{n_{11}}{K} - a\dfrac{n_{21}}{K}\right) \\ \dfrac{dn_{12}}{d\tau} = \left(\bar{k}n_{11} - kn_{12}\right) + \varepsilon r_1 n_{12}\left(1 - \dfrac{n_{12}}{K} - a\dfrac{n_{22}}{K}\right) \\ \dfrac{dn_{21}}{d\tau} = \left(-\bar{m}n_{21} + mn_{22}\right) + \varepsilon r_2 n_{21}\left(1 - b\dfrac{n_{11}}{K} - \dfrac{n_{21}}{K}\right) \\ \dfrac{dn_{22}}{d\tau} = \left(\bar{m}n_{21} - mn_{22}\right) + \varepsilon r_2 n_{22}\left(1 - b\dfrac{n_{12}}{K} - \dfrac{n_{22}}{K}\right) \end{cases} \quad (1)$$

To study this system we first apply aggregation methods to transform it into a reduced system with two ordinary differential equations governing the dynamics of the global variables: the total density of species 1, $n_1(t) = n_{11}(t) + n_{12}(t)$, and the total density of species 2, $n_2(t) = n_{21}(t) + n_{22}(t)$. Both are adequate candidates to global variables because they are constants of motion of the migration process, i.e., they keep constant at the fast time scale. If we forget the competitive interactions, global densities will not change but the distribution of each species between the two patches will evolve and tend towards certain equilibrium proportions. To calculate them let us suppose fixed values of n_1 and n_2 and find the equilibria of the fast part of system (1). We obtain for species 1

$$n_{11}^* = \frac{k}{k+\bar{k}} n_1 = \vartheta_1^* n_1 \quad \text{and} \quad n_{12}^* = \frac{\bar{k}}{k+\bar{k}} n_1 = \vartheta_2^* n_1 \quad (2)$$

and for species 2

$$n_{21}^* = \frac{m}{m+\bar{m}} n_2 = \mu_1^* n_2 \quad \text{and} \quad n_{22}^* = \frac{\bar{m}}{m+\bar{m}} n_2 = \mu_2^* n_2 \quad (3)$$

where constants ϑ_1^* and ϑ_2^* represent the fast equilibrium proportions of species 1 on each patch while the constants μ_1^* and μ_2^* represent the fast equilibrium proportions of species 2 on each patch. It is immediate to prove that these equilibria are stable for fast dynamics.

Now, coming back to the complete model (1), we can write a system for the two global variables just by adding up the corresponding equations and substituting the former state variables by the fast equilibria ((2), (3)) as follows:

$$n_{11} = \vartheta_1^* n_1\,,\ n_{12} = \vartheta_2^* n_1\,,\ n_{21} = \mu_1^* n_2 \text{ and } n_{22} = \mu_2^* n_2$$

Obtaining the following aggregated system at the slow time scale:

$$\begin{cases} \dfrac{dn_1}{dt} = r_1 n_1 \left(1 - \dfrac{\left(\vartheta_1^*\right)^2 + \left(\vartheta_2^*\right)^2}{K} n_1 - a \dfrac{\vartheta_1^* \mu_1^* + \vartheta_2^* \mu_2^*}{K} n_2 \right) \\ \dfrac{dn_2}{dt} = r_2 n_2 \left(1 - b \dfrac{\vartheta_1^* \mu_1^* + \vartheta_2^* \mu_2^*}{K} n_1 - \dfrac{\left(\mu_1^*\right)^2 + \left(\mu_2^*\right)^2}{K} n_2 \right) \end{cases} \tag{4}$$

According to aggregation methods (Auger et al. 2008a, Auger et al. 2008b), we can study the dynamics of the complete system (1) by carrying out the study of the aggregated model (4) (see appendix A).

The aggregated model (4) is a classical Lotka-Volterra competition model (Murray 2002) and its asymptotic behaviour is better described by performing the following change of variables:

$$u_1 = n_1 \frac{\left(\vartheta_1^*\right)^2 + \left(\vartheta_2^*\right)^2}{K} \text{ y } u_2 = n_2 \frac{\left(\mu_1^*\right)^2 + \left(\mu_2^*\right)^2}{K},$$

that yields

$$\begin{cases} \dfrac{du_1}{dt} = r_1 u_1 \left(1 - u_1 - a_{12} u_2\right) \\ \dfrac{du_2}{dt} = r_2 u_2 \left(1 - a_{21} u_1 - u_2\right) \end{cases}$$

where

$$a_{12} = a \frac{\vartheta_1^* \mu_1^* + \vartheta_2^* \mu_2^*}{\left(\mu_1^*\right)^2 + \left(\mu_2^*\right)^2} \text{ and } a_{21} = b \frac{\vartheta_1^* \mu_1^* + \vartheta_2^* \mu_2^*}{\left(\vartheta_1^*\right)^2 + \left(\vartheta_2^*\right)^2} \tag{5}$$

Now, the asymptotic behaviour of the solutions of system (4), i.e. the long term outcome of competition, is determined by the positive parameters a_{12} and a_{21} being greater or smaller than one (Murray 2002). If $a_{12} < 1$ (resp. $a_{21} < 1$) then species 1 (resp. 2) can invade when rare while it is excluded when rare for $a_{12} > 1$ (resp. $a_{21} > 1$). The possible outcomes of

competition are thus coexistence via niche partitioning if $a_{12}<1$ and $a_{21}<1$, exclusion via priority effects (the excluded species depend on initial conditions, the species that gains an early advantage wins) if $a_{12}>1$ and $a_{21}>1$, species 1 outcompetes species 2 if $a_{12}<1$ and $a_{21}>1$, and species 2 out-competes species 1 if $a_{12}>1$ and $a_{21}<1$.

2. Model analyses and results

We study the outcome of global competition in terms of the four independent parameters involved in the model. Firstly, a and b, representing competition abilities of species 2 and 1, respectively, which verify $a<1<b$ due to the assumption of local dominance of species 1 on species 2. Secondly, we represent migration through parameters ϑ_1^* and μ_1^* (called x and y, resp., in figures 1, 2 and 3) which are the proportions of species 1 and 2 in patch 1, respectively. The closer to 1 (resp. 0) these parameters are the more biased the distribution of the corresponding species is towards patch 1 (resp. 2) or, analogously, the greater the ratio $k/\bar{k}$ or $m/\bar{m}$, depending of the species, is (see appendix B for calculations).

The ability of species 1 to invade when rare depends on parameter a, which represents species 2 competitive ability, but it is independent of parameter b, which represents species 1 competitive ability. There is a threshold value $a^*=2\left(\sqrt{2}-1\right)\approx 0.8284$ so that if $a<a^*$ then species 1 can invade when rare for any values of migration parameters. Figure 1 shows in the migration parameter space the region (dark) for which species 1 is unable to invade when rare (values of a 0.75, 0.85 and 0.95). We find no region for $a=0.75<a^*$, for $a=0.85>a^*$ there are two small sub-regions -symmetric with respect to the point (0.5,0.5) because of the equivalence of the two patches-, that enlarge when $a=0.95$.

A similar analysis can be done to evaluate species 2 global invasibility -the local inferior competitor- , when rare. The only competition related parameter involved is b. For any value

of $b>1$, a region in the migration parameter space can be found for which species 2 can invade when rare. The size of this region decreases as expected for increasing values of species 1 competition ability b, (dark region in figure 2; $b=1.1$, $b=1.5$ and $b=2.5$). We notice that species 2 can never invade if it is almost uniformly distributed between patches. As b increases the range of distributions that prevent species 2 from invading also increases. Regions amenable to invasion exhibit an opposite distribution to that of species 1. That is, if species 1 has a fairly high competitive ability then species 2 invasion requires that the distribution of species 1 is clearly biased towards one of the patches while the distribution of species 2 is concentrated in the other patch.

To analyse the outcome of competition we need to consider simultaneously invasion and non-invasion regions for both species. If $a<a^*$ (region I of the parameters a and b space, fig. 4) the region of species 1 invasion is the whole migration parameter space and thus dark regions in figure 2 render species coexistence. The light region then indicates where species 1 outcompetes species 2.

To analyse the cases $a>a^*$ we examine the intersections between regions where species 1 cannot invade (fig. 1) with regions where species 2 can invade (fig. 2). In appendix B we prove that for each particular value of $a>a^*$ three different cases depending on b are found.

First we assume rather low b values, $b<b_*=1+a/2-\sqrt{a^2+4a-4}/2$ (region II of the parameters a and b space, fig. 4). We have then (fig. 3, $b=1.1$), that the region where species 1 cannot invade (white) is included in the region where species 2 invades, thus becoming a region (light) where the competition outcome results in species 1 exclusion. We also observe a coexistence region (dark) and a species 2 exclusion region (light grey).

For $b_*<b<b^*=1+a/2+\sqrt{a^2+4a-4}/2$ (region III of the parameters a and b space, fig. 4) the increase in b (fig. 3, $b=1.5$) entails that a part of the species 1 non-invasion region is

now included in the species 2 non-invasion region resulting in a new region (dark grey) where we find exclusion via priority effects.

The last case is when $b^* < b$ (region IV of the parameters a and b space, fig. 4). For these values (fig. 3, $b = 2.5$) the species 1 non-invasion region is now completely included in the species 2 non-invasion region and so there is no region of species 1 exclusion although it might be excluded in the dark grey region via priority effects.

3. Discussion

The issue of scale is a recurrent topic in the development of theoretical ecology. The metapopulation framework involves a specific recognition of the temporal scales at which ecological processes operate, with an explicit separation of within- and among patch dynamics (Amarasekare and Nisbet, 2001). When the migration process across patches operates at a faster scale relative to local dynamics the interplay of local dynamics and migration can differ from the case in which both processes operate at the same time scale.

The fact that migration acts at a faster scale than local dynamics brings new dimensions to metapopulation dynamics. Specifically, *previous* to local dynamics regulation each species distributes between patches proportionally to its own migration rates and therefore independently from migration rates of competing species and from both species demographic parameters. Once species distributions are set, then the outcome of competition depends on demographic parameters. When migration and local competitive interactions occur at the same time scale it is expected that under asymmetric competition the locally superior competitor (LSC) tends to dominate globally, this is particularly true in a homogeneous environment (Amarasekare and Nisbet, 2001). Notwithstanding, as we prove, the proposed time scale separation entails, for any values of competitive abilities, the existence of a range of migration strategies which outcome is coexistence. Also, when the competitive abilities of

the locally inferior competitor (LIC) and the LSC are not very far from each other, LIC can both locally and globally outcompete LSC depending on migration strategies. Thus migration traits should covary with competitive related traits to have an impact on species fitness.

Long et al. (2007) study the effects of immigration and environmental variability on the persistence of an inferior competitor by means of an experimental microcosm, proposing that this persistence in closed systems is possible if environmental variability makes a sink for the inferior competitor become temporally a source. We show through our mathematical model that this is also the case when the only environmental variability is due to changes in populations densities as a result of constant asymmetric migration rates.

In our model migration rates establish species distributions between patches and then parameters a, LIC competitive ability, and b, LSC competitive ability, decide the outcome of competition. Parameter a governs by itself the possibility of LSC invading when rare, if $a < a^* \approx 0.8284$ then it has no influence and LSC can invade in any case, on the other hand, for $a > a^*$ the closer a is to 1 the larger the choice of possible species distributions for which LSC cannot invade (fig. 1). In its turn, whether LIC can invade or not depends on parameter b; we stress that there always exists a region in the parameter space of species distributions where LIC can invade, so that the outcome of competition is either coexistence or exclusion of the LSC, and, as expected, the larger (resp. the closer to 1) b the smaller (resp. the larger) this region (fig. 2).

As a rule of thumb even distributions of species between patches (IFD would fall into this category) result in global dominance of the LSC. This LSC dominance may depend just in its own distribution, e.g., for a rather high LIC competitive ability $a = 0.9$ and a moderate LSC competitive ability $b = 1.5$, LIC is excluded, independently of its distribution, provided that LSC does not exceed 64% of its number in each patch (fig. 3). Also, if both species are skewed towards the same patch, what can be called coincident uneven distributions, LSC has

an advantage to outcompete LIC, e.g., even for a rather high $a = 0.9$ and low $b = 1.13$ LIC is excluded provided that $1/2 < \vartheta_1^* < \mu_1^* + 0.11$, that is, in the most inhabited patch the percentage of LIC is not below the percentage of LSC by more than 11%. Finally, if both species are skewed towards different patches there is a propensity to coexistence. The smaller b the larger is the region in the migration parameter space where coexistence is met; in the limit case, i.e. b approaching 1, general non coincident uneven distributions ($\vartheta_1^* < 1/2 < \mu_1^*$ or $\mu_1^* < 1/2 < \vartheta_1^*$) imply coexistence.

Let us remark here that in our setting, global coexistence implies local coexistence which is not the case in the patch occupancy metapopulation approach. Necessary conditions for LSC to be globally, and therefore locally, excluded are, on the one hand, that the competitive ability of LIC be rather high, $a > a^*$, and the one of LSC rather low $b < b^*$ (region II, fig. 4). On the other hand, there are also necessary conditions on both species between patches distributions that can be summarized, depending on the patch, as $1/2 < \mu_1^* < \vartheta_1^*$ (resp. $\vartheta_1^* < \mu_1^* < 1/2$), that is, both species distributions are skewed towards patch 1 (resp. 2) but LIC distribution is less skewed than the one of LSC ($b = 1.1$, fig. 3). These distributions conditions tend to be sufficient as a and b tend to 1, that is, their local competitive abilities tend to be equal to each other. With the same distributions considerations but with $b > b^*$ (region IV, fig. 4), LSC can still be excluded via priority effects. We can finally add that the same distributions with $a < a^*$ and b close to 1 give coexistence as outcome of competition.

When migration and competition take place at a similar time scale the existence of a refuge for the LIC species can lead to global coexistence (Amarasekare and Nisbet, 2001). In our setting, fast migration can create a refuge-like effect when species tend to concentrate in different patches. As we show in section 2 there is always a region in the parameter space of species distributions where LIC can invade.

We observe that fast migrations can also achieve dominance reversal, i.e. LSC can be excluded globally and thus locally. We state in section 2 the general conditions that in terms of asymmetric migrations rates and competition abilities must meet so that LIC species becomes the superior competitor on a spatially homogeneous environment. . Some other works show that in a spatially heterogeneous environment competitive reversal can be found with symmetric migration rates running on the same time scale than local dynamics (Takeuchi 1989; Takeuchi and Lu 1995). Other mechanisms of competitive reversal can also be found in competition models with continuous space and diffusion (Pacala and Roughgarden 1982, Cantrell et al 1998).

The key role of species distributions in final species dominance suggest a strong selective force for directed migration. Although adaptations linked to directed migration may be unlikely (Herrera 1985), directed migration may be a common phenomena even in the absence of adaptive traits (Wenny 2001). Specifically, directed migration may be ecologically meaningful if one migration vector has a disproportionate effect on plant recruitment (e.g. Purves et al 2007) which can improve species persistence in response to habitat loss (Montoya et al. 2008). As the metapopulation framework is applied to new problems and empirical evidence builds up key underlying assumptions are challenged. A number of biological processes can take place in which movement across patches can in fact operate at a faster time scale than local dynamics (Amarasekare 1998, 2000a, 2000b). Migration and competition processes can operate at similar temporal time scales and thus colonizing rates may influence the outcome of local competition (Amarasekare and Nisbet 2001). For example in long lived organisms such as trees, gene flow through pollination or migration can take place at a much faster time scale than selection process (García-Ramos & Kirkpatrick 1997). In host-parasite systems -in which the individual host is the patch- the interplay between within-patch and among-patch evolutionary dynamics drives the evolution of intermediate levels of virulence

(Levin and Pimentel 1981). Also, asymmetries in migration across patches can have profound implications for species global dominance. For example, preferential migration towards suitable habitat and towards unoccupied patches has important consequences for estimating species response to habitat loss which can be overestimated in the classical Levins (1969, 1970) model (Purves & Dushoff 2005)

The problem of aggregation is inextricably link to the problem of model simplicity (Levin 1992). Convenient separation of spatial and temporal scales is thus implicit in almost any analytical formulation. The challenge for any given system will be to determine the appropriate levels of aggregation and simplification of the system that provides an accurate representation of the biological scales implied and that are in agreement with experimental evidence.

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4. Acknowledgements

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Appendix A

Results in aggregation methods are valid provided there exists a large enough ratio of time scales. The analytical study of the necessary ratio has only been performed in the context of linear discrete systems (Sanz and Bravo de la Parra, 2002). For nonlinear systems, numerical simulations have shown in different applications (Nguyen-Huu et al, 2006; Auger et al., 2008; Poggiale et al., 2008; Nguyen-Huu et al, 2008; Auger et al., 2009) that the approximation is appropriate for a qualitative analysis whenever the ratio of the fast to the slow time scale, represented by ε, is less than 0.1. This ratio of one order of magnitude appears to be a reasonable assumption in many particular applications.

We include in figures 5 and 6 a more detailed simulation than those appearing in the mentioned references. For the same set of parameters values, taking $\varepsilon = 0.1$, and two different sets of initial conditions, we calculate numerically the solution of system (1) and the corresponding solution of system (4). Then, for each of the four state variables of system (1), we put together its evolution in time t and the one predicted by the aggregated system through the equalities $n_{11} = \vartheta_1^* n_1$, $n_{12} = \vartheta_2^* n_1$, $n_{21} = \mu_1^* n_2$ and $n_{22} = \mu_2^* n_2$. We can observe in figures 5 and 6 that the long term behaviour of both is very similar.

Appendix B

Firstly we study when species 1 can or cannot invade when rare. For that we need to solve $a_{12} < 1$ and $a_{12} > 1$ where we use the expression in (5) $a_{12} = a\left(\vartheta_1^* \mu_1^* + \vartheta_2^* \mu_2^*\right) / \left(\left(\mu_1^*\right)^2 + \left(\mu_2^*\right)^2\right)$. Let us do the notation changes $x = \vartheta_1^*$ and $y = \mu_1^*$, so $\vartheta_2^* = 1 - x$, $\mu_2^* = 1 - y$ and so $a_{12} = a\dfrac{x(2y-1) - y + 1}{2y^2 - 2y + 1}$. We now study the line $a_{12} = 1$ which can be written as an explicit function of x in terms of y:

$$x = f(y) = \frac{2y^2 + (a-2)y + (1-a)}{a(2y-1)}$$

The graph of f is symmetrical with respect to the point $(1/2,1/2)$, has two asymptotes: $y=1/2$ and $x=1/a(y-1/2)+1/2$, and it is composed of two branches which have a non-void intersection with the square $[0,1]\times[0,1]$ provided they exist real values of y for $x=0$. The roots of equation $2y^2+(a-2)y+(1-a)=0$ are $y_1=\frac{2-a-\sqrt{a^2+4a-4}}{4}$ and $y_2=\frac{2-a+\sqrt{a^2+4a-4}}{4}$ which are real if $a^2+4a-4>0$, that is

$$a \geq a^* = 2\left(\sqrt{2}-1\right)$$

For every $a > a^* = 2\left(\sqrt{2}-1\right)$ there are two symmetric regions enclosed by lines $x=f(y)$ and either $x=0$ or $x=1$ which corresponds to the solution of $a_{12}>1$, i.e. parameter values for which species 1 cannot invade when rare. The rest of the square $[0,1]\times[0,1]$ corresponds to the case of species 1 invasion.

A similar analysis can be done to study when species 2 can or cannot invade when rare. We need to solve $a_{21}<1$ and $a_{21}>1$, and so we look at the line $a_{21}=1$ which is expressed in terms of x and y as

$$y=g(x)=\frac{2x^2+(b-2)x+(1-b)}{b(2x-1)}.$$

The graph of g is also symmetrical with respect to the point $(1/2,1/2)$ and has two asymptotes and two branches. In this case it is straightforward to prove that the intersection with the square $[0,1]\times[0,1]$ exists for any value of $b>1$ and there are two symmetric regions surrounding points $(0,1)$ and $(1,0)$ which corresponds to the solution of $a_{21}<1$, parameter values for which species 2 invades when rare, letting the rest of the square $[0,1]\times[0,1]$ for the region of non invasion.

To obtain the parameter values regions corresponding to the different competition outcomes we need to put together the regions described previously. In particular we should find conditions so that those regions intersect. We know that line $a_{21}=1$ has the point $(0,y_3)=(0,(b-1)/b)$ on the y axis, The intersection between regions $a_{12}>1$ and $a_{21}<1$ depends on the relative position of y_3 with respect to y_1 and y_2: (i) if $y_3<y_1$ the region $a_{21}<1$ includes the region $a_{12}>1$; (ii) if $y_1<y_3<y_2$ there is an intersection without inclusions between regions $a_{21}<1$ and $a_{12}>1$; (iii) if $y_2<y_3$ there is no intersection between regions $a_{21}<1$ and $a_{12}>1$. To distinguish these three cases in terms of the values of parameters a and b we see when y_3 coincides with either y_1 or y_2 by substituting y_3 in $2y^2+(a-2)y+(1-a)=0$, thus obtaining:

$$b_*=1+a/2-\sqrt{a^2+4a-4}/2 \text{ and } b^*=1+a/2+\sqrt{a^2+4a-4}/2,$$

what yields case (i) if $1<b<b_*$, case (ii) if $b_*<b<b^*$ and case (iii) if $b^*<b$.

FIGURE LEGENDS

Figure 1: *Influence of species 2 competition ability, a, on species 1 being able to invade when rare.* Each diagram represents the space of parameters x, proportion in patch 1 of species 1, and y, proportion in patch 1 of species 2, i.e. the square $[0,1]\times[0,1]$. For three different values of a (0.75, 0.85 and 0.95) we draw in white the region where species 1 can invade and in black where it cannot.

Figure 2: *Influence of species 1 competition ability, b, on species 2 being able to invade when rare.* Each diagram represents the space of parameters x, proportion in patch 1 of species 1, and y, proportion in patch 1 of species 2, i.e. the square $[0,1]\times[0,1]$. For three different values of b (1.1, 1.5 and 2.5) we draw in black the region where species 2 can invade and in white where it cannot.

Competition outcomes for $a < a^* = 2\left(\sqrt{2}-1\right) \approx 0.8284$. For theses cases the same diagrams represent in black the regions of coexistence and in white the region of species 1 outcompeting species 2.

Figure 3: *Competition outcomes for* $a > a^* = 2\left(\sqrt{2}-1\right) \approx 0.8284$*: influence of* b. Each diagram represents the space of parameters x, proportion in patch 1 of species 1, and y, proportion in patch 1 of species 2, i.e. the square $[0,1]\times[0,1]$. For fixed $a = 0.9$ and three different values of b (1.1, 1.5 and 2.5) we draw in black the region where we find species coexistence, in light grey where species 1 outcompetes species 2, in white where species 2 outcompetes species 1 and in dark grey where there is exclusion via priority effects.

553 **Figure 4:** *Regions of the parameters a and b space with different competition diagrams in*
554 *terms of migration parameters.* Region I, $a \le a^*$, the diagram corresponds to the ones in
555 figure 2. Region II, $a > a^*$ and $1 < b < b_* = 1 + a/2 - \sqrt{a^2 + 4a - 4}/2$, the diagram corresponds to
556 the one in figure 3 $b = 1.1$. Region III, $a > a^*$ and $b_* < b < b^* = 1 + a/2 + \sqrt{a^2 + 4a - 4}/2$, the
557 diagram corresponds to the one in figure 3 $b = 1.5$. Region IV, $a > a^*$ and $b^* < b$, the diagram
558 corresponds to the one in figure 3 $b = 2.5$.
559
560 **Figure 5.** *Comparison of solutions of system (2) with their approximations through the*
561 *aggregated system (5).* This figure shows the evolutions in time of each of the four state
562 variables of system (1) (n_{11}, n_{12}, n_{21} and n_{22}) and their approximations obtained from the
563 aggregated system (4) ($\vartheta_1^* n_1$, $\vartheta_2^* n_1$, $\mu_1^* n_2$ and $\mu_2^* n_2$, respectively) for the parameters values
564 $\varepsilon = 0.1$, $k = 0.9$, $\bar{k} = 0.1$, $m = 0.7$, $\bar{m} = 0.3$, $r_1 = 0.3$, $r_2 = 0.2$, $K = 5$, $a = 0.9$ and $b = 1.5$,
565 and initial conditions $n_{11}(0) = 0.7$, $n_{12}(0) = 0.3$, $n_{21}(0) = 0.4$ and $n_{22}(0) = 0.6$.
566
567 **Figure 6.** *Comparison of solutions of system (2) with their approximations through the*
568 *aggregated system (5).* This figure shows the evolutions in time of each of the four state
569 variables of system (1) (n_{11}, n_{12}, n_{21} and n_{22}) and their approximations obtained from the
570 aggregated system (4) ($\vartheta_1^* n_1$, $\vartheta_2^* n_1$, $\mu_1^* n_2$ and $\mu_2^* n_2$, respectively) for the same parameters
571 values as in figure 5 and initial conditions $n_{11}(0) = 0.2$, $n_{12}(0) = 0.3$, $n_{21}(0) = 4$ and
572 $n_{22}(0) = 6$.
573

575

576 **Figure 1**

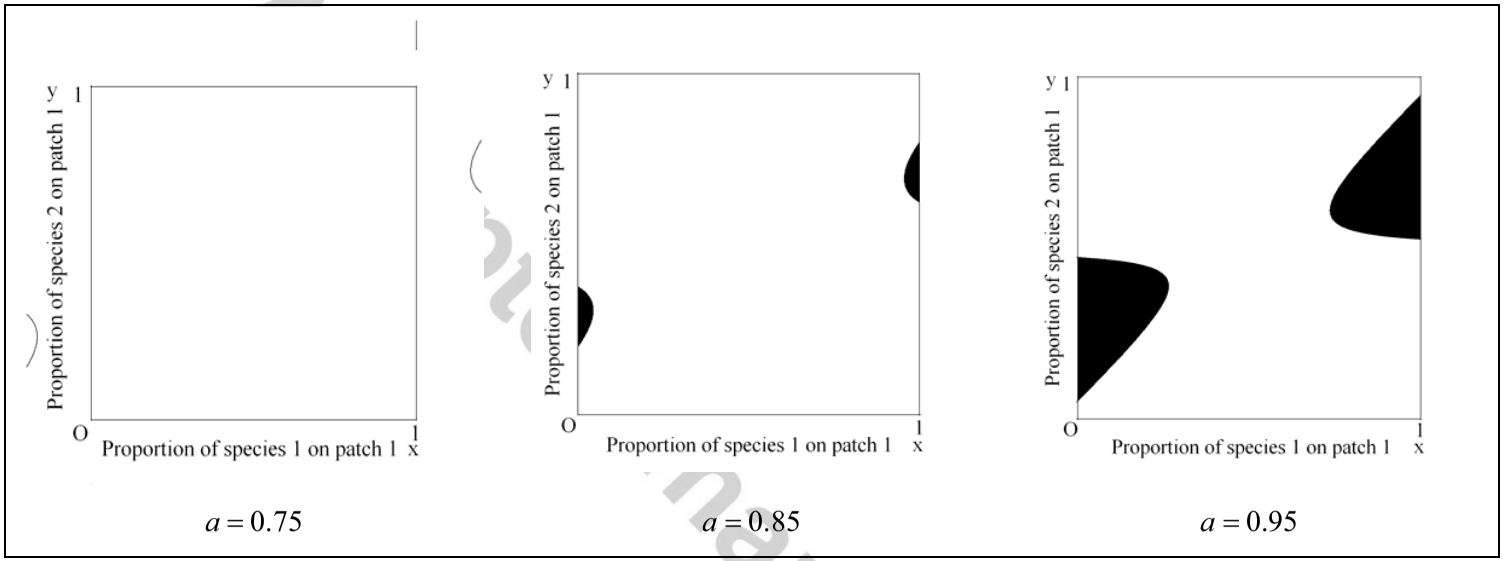
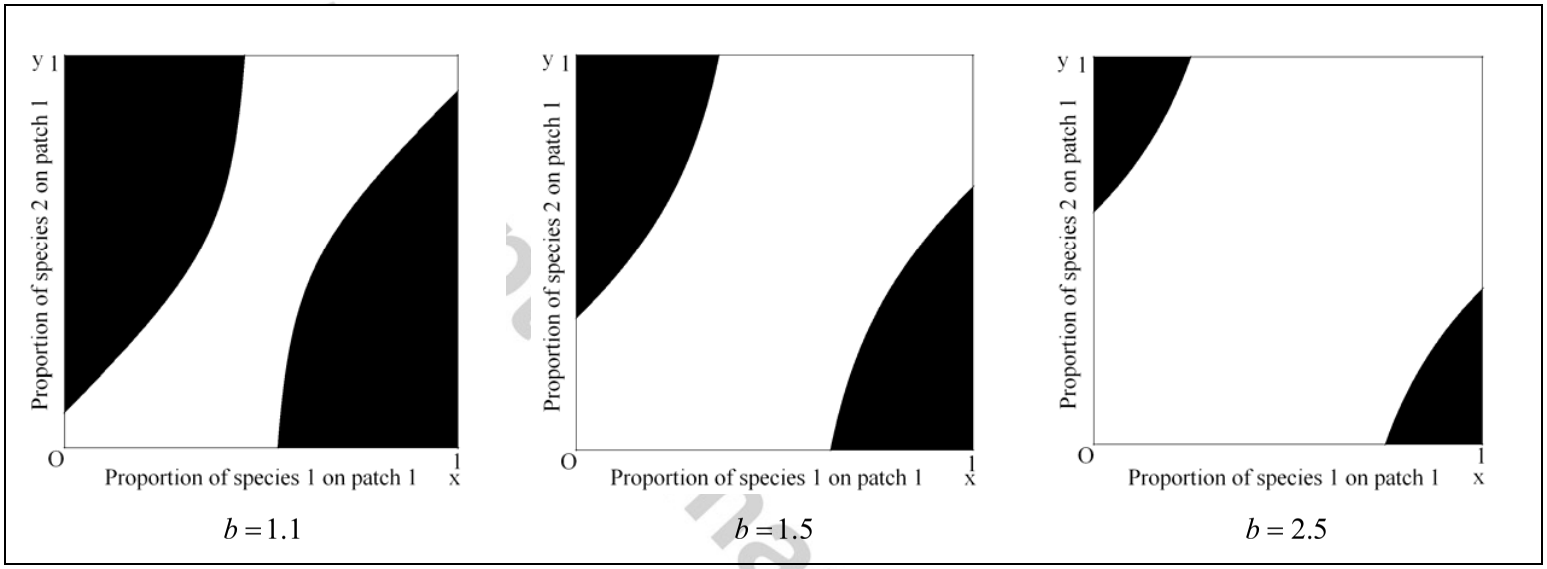


Figure 2



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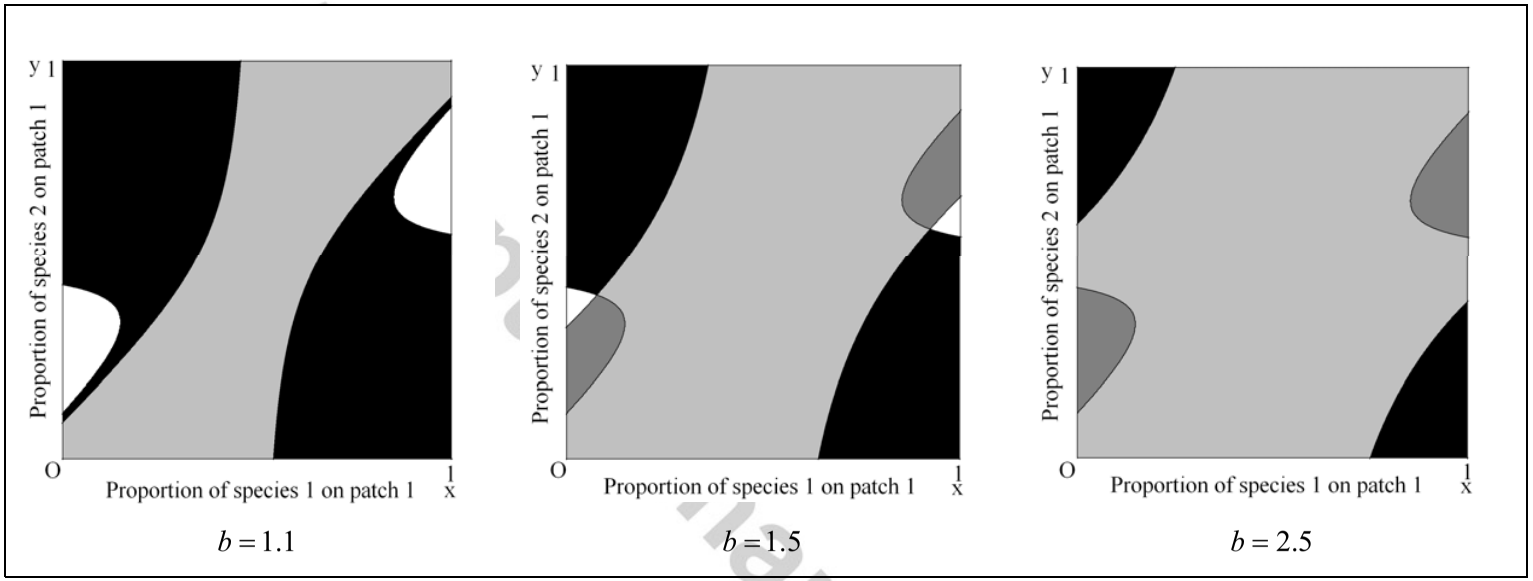

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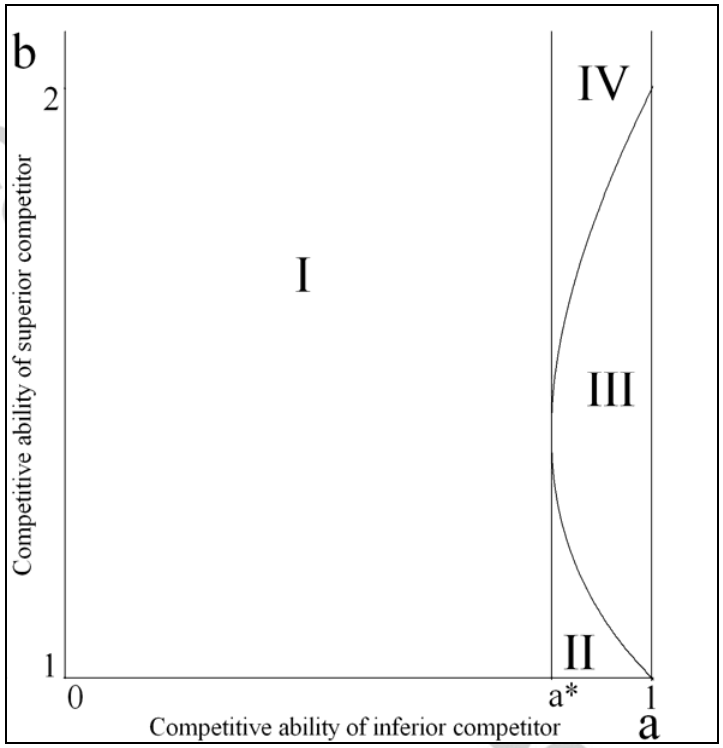
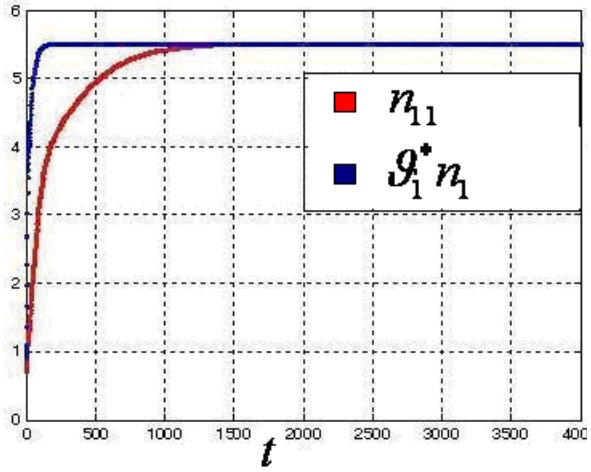


Figure 5



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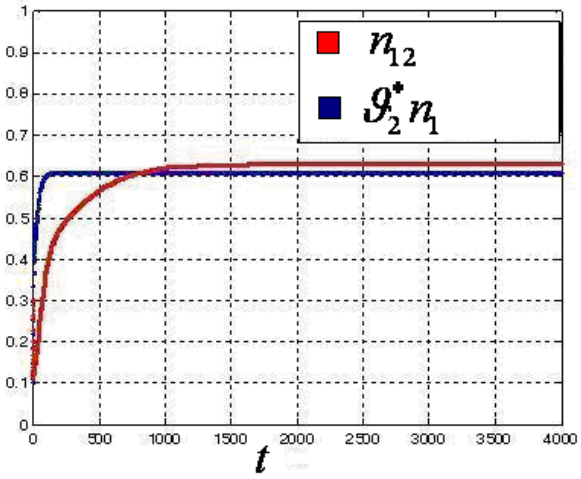

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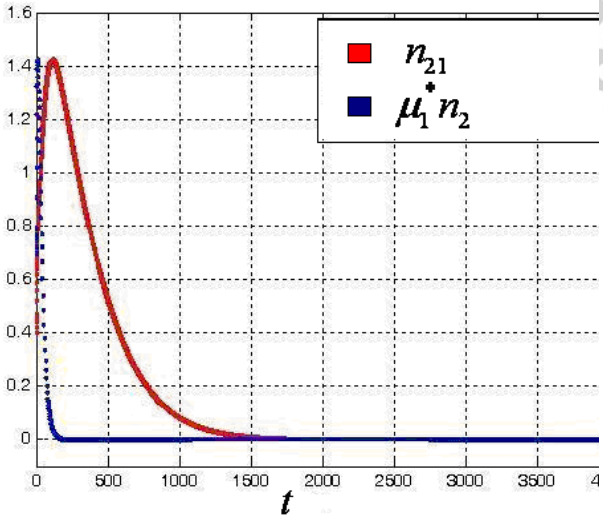

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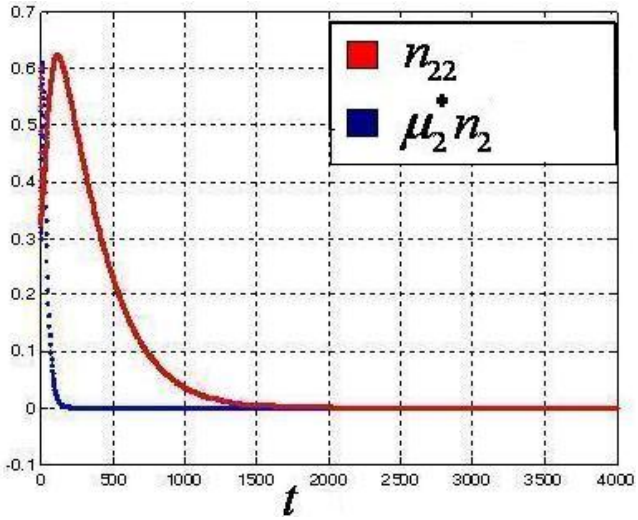

(d)

Figure 6