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Abstract:
Although density-dependent dispersal and relative dispersal (the difference in dispersal rates between species) have been documented in natural systems, their effects on the stability of metacommunities are poorly understood. Here we investigate the effects of intra- and interspecific density-dependent dispersal on the regional stability in a predator-prey metacommunity model. We show that, when the dynamics of the populations reach equilibrium, the stability of the metacommunity is not affected by density-dependent dispersal. However, the regional stability, measured as the regional variability or the persistence, can be modified by density-dependent dispersal when local populations fluctuate over time. Moreover these effects depend on the relative dispersal of the predator and the prey. Regional stability is modified through changes in spatial synchrony. Interspecific density-dependent dispersal always desynchronises local dynamics, whereas intraspecific density-dependent dispersal may either synchronise or desynchronise it depending on dispersal rates. Moreover, intra- and interspecific density-dependent dispersal strengthen the top-down control of the prey by the predator at intermediate dispersal rates. As a consequence the regional stability of the metacommunity is increased at intermediate dispersal rates. Our results show that density-dependent dispersal and relative dispersal of species are keys to understanding the response of ecosystems to fragmentation.

Keywords:
dispersal behaviours, spatial synchrony, top-down control, regional variability, persistence

INTRODUCTION

Understanding the mechanisms that govern the stability of metacommunities is a key challenge to understand the response of ecosystems to fragmentation. Metacommunities are regional sets of local communities linked by dispersal, i.e., by the movement of individuals from a patch (emigration) to another (immigration) (Leibold *et al*. 2004). Both local and regional processes affect the stability of metacommunities. For instance, in predator-prey metacommunities, local processes such as local density regulation mechanisms drive local predator-prey population fluctuations, which may lead to local extinctions when communities are isolated (Gause 1934; Lotka 1925; Rosenzweig and MacArthur 1963; Volterra 1926). But dispersal, which is a regional process, may allow regional persistence of the prey and the predator (Huffaker 1958) because it allows recolonization of vacant patches (Levins 1970) or rescue effects (Brown and Kodric-Brown 1977). This positive effect of dispersal on the regional stability of predator-prey metacommunities requires that dynamics are spatially asynchronous. If local populations fluctuate strongly and synchronously, the whole metapopulation may go extinct because of simultaneous extinction of local populations. But if fluctuations of local densities are asynchronous, recolonizations or rescue effects can occur and the persistence and stability of the metacommunity is improved (Comins and Blatt 1974; Hassell *et al*. 1991; Jansen 2001).

But dispersal and synchrony between communities are not independent processes. On the one hand, dispersal may increase spatial synchrony because exchanges of individuals between communities tend to reduce differences in population sizes, especially when dispersal is high (Bjornstad *et al*. 1999). On the other hand, weak dispersal may also synchronise dynamics in predator-prey metacommunities with nonlinear density regulation (Bjornstad 2000; Jansen 1999). Thus, both dispersal and local density regulation can

synchronise community dynamics. Since there is empirical evidence for asynchronous spatial dynamics in predator-prey metacommunities (Holyoak and Lawler 1996a; Holyoak and Lawler 1996b; Janssen *et al*. 1997; Nachman 1991; van de Klashorst *et al*. 1992), some mechanisms maintain persistent differences between local densities and counteract the synchronising effect of dispersal. These mechanisms have been explored using a number of models, and involve either stochastic or deterministic processes. Asynchrony between patches of the same quality can be due to independent stochastic local factors (Taylor 1990), such as demographic stochasticity in small populations (Nachman 1987a) and stochasticity of dispersal between patches or of environmental variations in population parameters (Crowley 1981; Reeve 1988; Reeve 1990). These models show that an intermediate dispersal intensity of the prey and the predator insures metacommunity persistence (Crowley 1981; Nachman 1987b; Nachman 1991; Reeve 1988; Zeigler 1977 reviewed in Holyoak and Lawler 1996b). Dispersal must be sufficiently high to allow recolonization of extinct patches, but sufficiently low to maintain the desynchronising effect of stochastic local processes. Spatial asynchrony can also emerge from the interaction between local dynamics and dispersal (Jansen 1995). In deterministic predator-prey metacommunities with nonlinear density regulation, spatial asynchrony between patches arises when dispersal rates are either low or intermediate. In these models, population dynamics are synchronous when dispersal is high, and temporal variation in regional densities is decreased when dispersal rates are decreased.

In this paper, we investigate the influence of two key aspects of dispersal behaviours on the stability of predator-prey metacommunities: the density dependence in dispersal, and the ratio of predator and prey dispersal rates, which we name "relative dispersal". Density-dependent dispersal, i.e. dispersal changes in response to changes of species densities in the donor patch, has been observed in several experimental systems (see for instance Bernstein

1984; French and Travis 2001; Hauzy *et al*. 2007). It implies a direct effect of local processes (population dynamics) on regional processes (dispersal). A species' population density can affect its own dispersal (intraspecific density-dependent dispersal) or the dispersal of another species (interspecific density-dependent dispersal). Recent models including density-dependent dispersal in predator-prey metacommunities yielded contrasted results. McCann *et al.* (2000) suggested that local predator population outbreaks do not depend on interspecific density-dependent dispersal. By contrast, Li *et al.* (2005) showed that interspecific density-dependent dispersal can reduce spatial synchrony in both the prey and the predator. Most of these studies, however, have assumed that prey and predator dispersal rates are equal. But empirical data suggest that dispersal abilities of prey and predator can be very different. The large range of predator-prey body-size ratios observed in real food webs (Brose *et al*. 2006) and the allometric relationship between body size and the scale of species' movements (Rooney *et al*. 2008) or dispersal abilities (Jenkins *et al*. 2007) suggest that the relative dispersal rate of the predator compared to the prey can vary within a large range. In some ecosystems, scale of movement is strongly positively related to trophic position, suggesting a higher dispersal rate for the predator than for the prey. In other systems, predators can even be less mobile than their prey, suggesting a higher dispersal rate for the prey than for the predator. Differences in the dispersal abilities of the prey and the predator can have important consequences, and yet have received little attention so far.

Here we develop a deterministic metacommunity model of a prey and a predator that includes density-dependent dispersal. We compare the effects of both intra- and interspecific density-dependent dispersal on the dynamics and the stability of the prey and the predator at the regional scale with those of constant dispersal. We study the effects of density-dependent dispersal in two contrasting cases of relative dispersal: either predator dispersal is distinctly higher than prey dispersal or prey dispersal is distinctly higher than

predator dispersal. These comparisons allow us to assess the effects of density-dependent dispersal and relative dispersal on the relationship between dispersal and the stability of predator-prey metacommunities.

THE MODEL

We consider a patchy landscape consisting of several localities. Each locality is occupied by a local predator-prey community. Within each community, local dynamics follow a Rosenzweig–MacArthur predator-prey model (Rosenzweig and MacArthur 1963): prey growth is logistic, the predator has a Holling type II functional response and its mortality rate is constant. Local communities are linked by dispersal of both species from one patch to another. A collection of such communities constitutes a predator-prey metacommunity. For the sake of simplicity, and following Jansen (1995, 2001), we study a 2-patch predator-prey metacommunity in which the two patches are identical. The dynamics of the prey and the predator in the two patches (1 and 2) are given by a system of ordinary differential equations:

$$\begin{cases} \dfrac{dN_1}{dt} = r N_1\left(1-\dfrac{N_1}{K}\right) - \dfrac{b N_1 P_1}{c+N_1} - N_1\, D_n(N_1,P_1) + N_2\, D_n(N_2,P_2) \\ \dfrac{dP_1}{dt} = \dfrac{b N_1 P_1}{c+N_1} - m P_1 - P_1\, D_p(N_1,P_1) + P_2\, D_p(N_2,P_2) \\ \dfrac{dN_2}{dt} = r N_2\left(1-\dfrac{N_2}{K}\right) - \dfrac{b N_2 P_2}{c+N_2} - N_2\, D_n(N_2,P_2) + N_1\, D_n(N_1,P_1) \\ \dfrac{dP_2}{dt} = \dfrac{b N_2 P_2}{c+N_2} - m P_2 - P_2\, D_p(N_2,P_2) + P_1\, D_p(N_1,P_1) \end{cases} \quad (1)$$

where N_i and P_i denote the population densities of the prey and the predator, respectively, in patch i =1, 2. As patches are identical, species parameters are the same in both patches. r and K denote the growth rate and carrying capacity of the prey; b and c are the saturation value and the half-saturation constant of the predator functional response; m is the predator mortality rate. Conversion efficiency from prey to predator has been set to 1. This does not

constitute an ecological assumption but arises from a simple mathematical rescaling of N_i or P_i.

The last two terms of equations describe dispersal from and to each patch. We make the ecological hypothesis that migration is not costly; as a consequence, the emigration term in one patch corresponds exactly to the immigration term in the other. This assumption fits in well with dispersal through corridors that allow fast moves with limited mortality risks. Dispersal rates are determined locally: the *per capita* dispersal rates from patch *i* of the prey $D_n(N_i, P_i)$ and of the predator $D_p(N_i, P_i)$ are functions of species densities in the donor patch *i* only. The dispersal rate of each species may depend on its own local density, which we refer to as "intraspecific density-dependent dispersal", and on the local density of the other species, which we refer to as "interspecific density-dependent dispersal" (Hauzy *et al*. 2007). Our mathematical analysis deals with the general model, but our numerical simulations investigate the separate effects of intraspecific and interspecific density dependence in dispersal. The dispersal rates then simplify into $D_n(N_i)$ or $D_n(P_i)$ and $D_p(P_i)$ or $D_p(N_i)$. In numerical simulations, density dependence in dispersal is modelled through Hill functions, which have been chosen for their convenient plasticity: the *per capita* dispersal rate from patch *i* of the prey writes

$$D_n(N_i) = d_n \frac{N_i^{x_{nn}}}{S_{nn}^{x_{nn}} + N_i^{x_{nn}}} \quad \text{or} \quad D_n(P_i) = d_n \frac{P_i^{x_{np}}}{S_{np}^{x_{np}} + P_i^{x_{np}}}$$

and the *per capita* dispersal rate of the predators writes

$$D_p(P_i) = d_p \frac{P_i^{x_{pp}}}{S_{pp}^{x_{pp}} + P_i^{x_{pp}}} \quad \text{or} \quad D_p(N_i) = d_p \frac{N_i^{x_{pn}}}{S_{pn}^{x_{pn}} + N_i^{x_{pn}}}.$$

These formulations imply several assumptions. Species have a maximal *per capita* dispersal rate d_n for the prey, and d_p for the predator (fig. 1). These parameters can reflect

the ability of the species to disperse or the distance between patches. The half-saturation parameters $S_{\alpha\beta}$ are the densities of species β (prey: β stands for *"n"*; or predators: β stands for *"p"*) for which the *per capita* dispersal rates D_α of species α (α = *"n"*, *"p"*) is half of the maximal *per capita* dispersal rate d_α. Parameters $x_{\alpha\beta}$ determine the shape of density dependence in dispersal. When $x_{\alpha\beta} = 0$, dispersal is independent of density and occurs at a constant *per capita* rate $d_\alpha/2$; when $x_{\alpha\beta} > 0$, the dispersal rates increase with density; whereas when $x_{\alpha\beta} < 0$, they decrease with density. The absolute value of $x_{\alpha\beta}$ determines the steepness of density dependence: when $|x_{\alpha\beta}| = 1$, dispersal rates are concave functions of density up to their saturation level (cyrtoid shape), whereas they are sigmoidal when $|x_{\alpha\beta}| > 1$ (the inflexion point of the dispersal function then occurs at the threshold density $S_{\alpha\beta}$); high values of $|x_{\alpha\beta}|$ model step-like sigmoid curves, whereas low values model smoother variations in dispersal with population density.

In this paper, we explore density-dependent dispersal behaviours that mimic those observed in several experiments (Bernstein 1984; French and Travis 2001; Hauzy *et al*. 2007), i.e., prey dispersal increases with prey and predator densities (positive intra- and interspecific density-dependent dispersal in the prey), and predator dispersal increases with predator density (positive intraspecific density-dependent dispersal in the predator) and decreases with prey density (negative interspecific density-dependent dispersal in the predator). In terms of model parameters, this implies $x_{nn} > 0$, $x_{np} > 0$, $x_{pp} > 0$ and $x_{pn} < 0$. We conduct both a mathematical and a numerical analysis of the model.

MATHEMATICAL ANALYSIS

Stability of the symmetric equilibrium

We first focus on equilibriums of the model, and more specifically on the symmetric equilibrium, i.e., that for which densities are equal in patches 1 and 2 ($N_1=N_2$ and $P_1=P_2$). We analyse the stability of this equilibrium using the linearization method developed by Jansen (1994). The original method considers a predator-prey metacommunity model with constant dispersal. We extend the method to general forms of density-dependent dispersal and apply it to our model (Appendix A).

The stability of the symmetrical equilibrium depends only on the local parameters r, b, c, m and K. The equilibrium is stable if and only if the prey carrying capacity K is below a threshold value: $K < c(b+m)/(b-m)$ (Appendix A). For higher values of the prey carrying capacity, it is always unstable and a stable limit cycle appears. These results for density-dependent dispersal generalize those obtained for constant dispersal by Jansen (1995) and correspond to the well-known paradox of enrichment in the non-spatial MacArthur-Rosenzweig model. Neither prey nor predator dispersal affects the stability of the symmetric equilibrium and this conclusion is unaffected by density dependence in dispersal. A metacommunity exhibits the same sudden destabilisation of its dynamics when K increases beyond its threshold whether dispersal is constant or density dependent.

Regional densities at the symmetric equilibrium

Next, we analyse the effect of density-dependent dispersal on the total (regional) population densities of the prey and the predator at the symmetric equilibrium. From equations (1), we see that emigration from patch *i* and immigration to patch *i* cancel each other out for each species, so that the regional densities of the prey and the predator are independent of dispersal. Thus, prey and predator densities at the symmetric equilibrium are unaffected as well by dispersal (Jansen 1995), whether dispersal is constant or density dependent. When the metacommunity has reached equilibrium, local population densities are the same as in isolated communities. Asymptotic population densities at the symmetric equilibrium depend only on local processes. In our two-patch predator-prey metacommunity, when *K* is below the instability threshold, the asymptotic regional densities are simply equal to the values they would have in an isolated patch.

NUMERICAL ANALYSIS

When $K > c(b+m)/(b-m)$, There is no stable equilibrium any longer, and the prey and the predator show persistent oscillations through time. We used numerical simulations to investigate the effect of density-dependent dispersal on prey and predator asymptotic dynamics at the scale of the metacommunity.

Methods

We studied the various types of dispersal separately, *i.e.*, we studied constant dispersal in both species, intraspecific density-dependent dispersal in either the prey or the predator, and interspecific density-dependent dispersal in either the prey or the predator. For each of these five types of dispersal, we also studied two contrasting relative dispersal rates, one in which the maximal dispersal rate of the predator, d_p, is lower than that of the prey, d_n ($d_p = 0.01\ d_n$) and one in which the converse is true ($d_p = 100\ d_n$). Maximal dispersal rates varied between 10^{-4} and 10^{2} when $d_n > d_p$, and between 10^{-6} and 10^{0} when $d_p > d_n$. Within these ranges, we took 1000 sample values of each parameter (keeping the ratio d_n/d_p constant), uniformly distributed on a log scale. The parameters of local interactions were the following: r=10, K=25, b=11, c=1, m=10. For the density dependence in dispersal, we focused the numerical analysis on sigmoidal shapes ($|x_{\alpha\beta}|$=4, α=n,p ; β=n,p) and on values for the half-saturation parameters $S_{\alpha\beta}$ set close to the mean densities observed when populations are isolated: S_{nn}=S_{pn}=18 and S_{np}=S_{pp}=2.

The system of ordinary differential equations (1) was numerically simulated by means of C programs using the GNU Scientific Library. Numerical integrations used the embedded Runge-Kutta Prince-Dormand method. Based on preliminary inspection of numerous simulations, we estimated a time delay before population dynamics entered its

asymptotic regime. This "asymptotic time" (t_{asympt}) was much wider for low dispersal rates; it was then to 2 x 10^4 time units for high dispersal rates (Min (d_n , d_p) > 10^{-4}) and 2 x 10^5 time units for low dispersal rates (Min (d_n , d_p) < 10^{-4}). Our results were obtained from population dynamics observed between t_{asympt} and t_{asympt} + 10^4, except for the first Lyapunov exponent (see below), which was calculated on dynamics between t_{asympt} + 10^4 and t_{asympt} + 2.10^4.

All the variables and statistics considered in this study are related to the asymptotic dynamical regime and are computed on the attractors reached by population dynamics. Therefore, we needed a method to detect and follow the system's attractors as some control parameter (here, the maximal dispersal rates) is varied within a study interval. Except for catastrophic changes in the configuration of attractors, smooth variations in control parameters generate smooth "continuation branches", which correspond to the curves (or pieces of curves) shown on figures 2, 3, 4, 5, S3 and S4. Our model is complicated by the possibility of multiple coexisting attractors and chaotic regimes. Instead of using techniques based on numerical continuation of attractors (Kuznetsov 2004), which proved inefficient and intractable, we used a "sieve" technique of exploration, followed by the *ex post facto* reconstruction of "continuation branches". For each parameter value, the initial densities of the prey and the predator in the two patches were randomly sampled within ranges [0;20] for the prey and [0;10] for the predator as these ranges were commonly observed in the numerical simulations. This random sampling allowed us to explore the various basins of attraction of the possibly multiple attractors, and hence to detect the main attractors (i.e., those with a wide enough basin of attraction) by means of simulations runs from these initial population densities. The drawback of this method is that only one initial condition is simulated for each set of parameter values, so that in the case of multiple coexisting attractors, only one of them is reached. But, provided that parameter values are sampled densely enough in the study interval (we used a fine 1000-values sampling grid for the

maximal dispersal rates), the other attractors are very likely to be detected for neighboring values of the parameter. This eventually results in a slightly scattered general portrait of the various "continuation branches". The portrait "gaps" are then filled out by linking pairs of detected attractors, provided that parameter values are not too distant and the attractors are close enough in the state space. Attractor closeness was measured by means of the Hausdorff distance in $\Re^4$.

Analyses of dynamics were performed under the Matlab environment (R2008a). We studied two aspects of metacommunity dynamics: (1) the nature of the attractor, and (2) the degree of spatial synchrony. First, we determined whether population fluctuations were periodic or chaotic by numerically estimating the first Lyapunov exponent. Computation of the Lyapunov exponent in fast oscillating models like ours gives easily rise to an important computational error accumulation. For the sake of numerical accuracy, the first Lyapunov exponent was estimated on a Poincaré section of the orbit, as the exponential increase of deviations from the iterations of the Poincaré map (Wolf *et al*. 1985). In each simulation, we computed the Poincaré section that intersects the trajectory orthogonally at the asymptotic time t_{asympt}. We checked that the 10^4-time-unit interval we used to compute the Lyapunov exponent provided satisfactory converge of the estimate. A positive value of the first Lyapunov exponent reveals a chaotic attractor, while a negative value indicates a stable equilibrium on the Poincaré map, which corresponds to a stable limit cycle for the population dynamics in $\Re^4$. Second, to quantify the effects of dispersal behaviours on spatial synchrony in the asymptotic regime, we used the Pearson moment correlation coefficient between local densities in the two patches. As an alternative synchrony estimate, the correlation of the *per capita* population growth rates is recommended when population dynamics exhibits long-term transient trends, as often encountered in field or experimental measurements (Bjornstad *et al*. 1999). But as we studied the asymptotic regime here, Pearson correlation between local densities is appropriate. The higher spatial synchrony, the

closer to 1 the correlation coefficient. We investigated spatial synchrony for both the prey and the predator.

Because many definitions of stability exist in the literature (see e.g. a review in Loreau *et al*. 2002), the stability of the metacommunity can be defined in several ways. Two stability properties are regional persistence and the temporal variability of regional densities. Because our model is purely deterministic and does not allow for extinctions, persistence cannot be estimated directly. Persistence is here assessed indirectly by means of the minimal regional densities reached in the asymptotic regime; the lower these minimal densities, the higher the vulnerability of species to stochastic extinction, and the lower the probability of persistence. Results are presented in the supplementary material (supplementary material, fig. S3 and S4). We also measured the temporal variability of regional densities by their coefficient of variation (CV). To disentangle the effects of the temporal mean of regional densities and of their standard deviation, however, we present both the temporal mean and the CV of regional densities. Stability increases when the CV decreases.

In order to investigate the robustness of our results with regard to changes in dispersal parameters, we used a factorial design in which the independent variables were the shape of the density dependence of the dispersal rates ($|x_{\alpha\beta}|$), their half-saturation parameters ($S_{\alpha\beta}$), and their maximal values for both the prey and the predator (d_n and d_p). We compared two different shapes, cyrtoid ($|x_{\alpha\beta}|=1$) and sigmoid ($|x_{\alpha\beta}|=4$). We varied the half-saturation parameters $S_{\alpha\beta}$ by 20% above and below the mean densities when population are isolated ($S_{nn}=S_{pn}=18$ and $S_{np}=S_{pp}=2$). We also varied the maximal dispersal rates of the prey (d_n) and the predator (d_p) between 10^{-6} and 10^{2}. Within this range, we took a sample of 100 values for each parameter d_n and d_p (and up to 200 values for the reference parameter combination $|x_{\alpha\beta}|=4$, $S_{nn}=S_{pn}=18$ and $S_{np}=S_{pp}=2$), uniformly distributed on a log scale (see supplementary material, fig. S1 and S2).

Metacommunity dynamics

We first focus on two descriptors of metacommunity dynamics, the nature of the dynamics (chaotic or periodic), and the spatial synchrony between patches. The first Lyapunov exponent characterises the nature of dynamics of the whole community. The dynamics of the two species cannot be separated; they are either both periodic or both chaotic. Spatial synchrony was calculated for each species separately, but proved to be completely similar between the prey and the predator in all simulations. Therefore we present below results for spatial synchrony of the prey only. For the sake of simplicity, we present results for two contrasted relative dispersal rates but these results are robust to wide variations in relative dispersal rates (supplementary material, fig. S1 and S2). The different shapes ($x_{\alpha\beta}$) and half-saturation values ($S_{\alpha\beta}$) of density dependence give qualitatively the same results for each type of dispersal, except for intraspecific density-dependent dispersal in the prey, which is sensitive to $|x_{\alpha\beta}|$ (supplementary material, fig. S2). Below, we present the results for $|x_{\alpha\beta}|=4$ and mention when they are different for $|x_{\alpha\beta}|=1$.

At high dispersal rates, population dynamics are synchronous and periodic for all types of dispersal behaviours (fig. 2). The metacommunity model is then equivalent to a non-spatial predator-prey model. In contrast, at low and intermediate dispersal rates, synchrony depends both on the relative dispersal rate of the prey and the predator and on the type of dispersal.

When dispersal is density-independent (constant) and higher in the prey than in the predator (fig. 2A), spatial synchrony decreases monotonically with dispersal decrease, through both desynchronisation of periodic dynamics and the emergence of chaotic dynamics at intermediate dispersal rate. This decrease is rather low and the minimum value

of synchrony is still high. In contrast, when predator dispersal is higher than prey dispersal (fig. 2D), the dynamics can remain perfectly synchronous for all dispersal rates or become very asynchronous, provided that the dispersal rates are not too high. Indeed, for low and intermediate dispersal rates, the metacommunity dynamics shows two coexisting periodic attractors, the first one characterized by a perfect spatial synchrony while the second one shows a strong asynchrony between patches. The synchrony of the later decreases with increasing dispersal rates until the attractor disappears, letting the synchronous attractor alone. This coexistence of synchronous and asynchronous attractors has been observed by Jansen (1995). No chaotic dynamics is observed for this relative dispersal rate.

Density-dependent dispersal in the prey (fig. 2B, 2E) affects the dynamics only when prey dispersal is higher than predator dispersal ($d_n > d_p$) (fig. 2B). When predator dispersal is higher than prey dispersal ($d_p > d_n$) (fig. 2E), the dynamics is very similar to the case where dispersal is constant (fig. 2D). When $d_n > d_p$, intra- and interspecific density-dependent dispersal in the prey have different effects on spatial synchrony (fig. 2B). Intraspecific density-dependent dispersal synchronises local dynamics when dynamics are periodic (at low and intermediate dispersal rates), whereas spatial synchrony is decreased when dynamics are chaotic. The presence of the synchronising effect of intraspecific density-dependent dispersal does not depend on the shape of density dependence in dispersal ($|x_{\alpha\beta}|$=4: fig. 2B; $|x_{\alpha\beta}|$=1: Appendix B, fig. 5A), but the presence of chaotic dynamics does. When $|x_{\alpha\beta}|$=4 chaotic dynamics arise for a wider range of dispersal rates than when dispersal is constant (fig. 2A, 2B) whereas when $|x_{\alpha\beta}|$=1 chaotic dynamics disappear (Appendix B, fig. 5A). On the contrary, when prey dispersal is subject to interspecific density dependence, population dynamics are strongly desynchronised whether the dynamics be periodic or chaotic (fig. 2B).

Whatever the relative dispersal rates, intraspecific density-dependent dispersal in the predator does not affect spatial synchrony (fig. 2C, 2F). The effect of density-dependence in

predator dispersal shows up when it is interspecific and when predator dispersal is higher than prey dispersal (fig. 2F). Indeed, the bistable regime observed for constant dispersal disappears through the loss of the synchronous limit cycle. For low and intermediate dispersal rates, the remaining limit cycle shows strong asynchronous dynamics. The dynamics abruptly become synchronous at intermediate dispersal rate and the transition is accompanied with the emergence of a new chaotic window. Thus, for interspecific density-dependent dispersal in the predator, spatial synchrony dependence upon dispersal rate simplifies into a global increasing relationship.

Regional densities

The temporal mean of regional densities of the prey and the predator are affected by dispersal rates in the same way for all types of dispersal behaviour and of relative dispersal. For the same range of dispersal rates, prey regional density decreases (fig. 3) while predator regional density increases (fig. 4) in a correlated way. This suggests that dispersal modifies the strength of the impact of predator populations on prey populations at the regional scale. First, changes in prey and predator regional densities occur for dispersal rate in chaotic windows and for dispersal rate close to chaotic window but at which dynamics are periodic (fig. 3A, 3B, 3C, 3F; fig. 4A, 4B, 4C, 4F). Second, these changes occur for asynchronous limit cycle which exists when predator dispersal is higher than prey's one (fig. 3D, 3E, 3F; fig. 4D, 4E, 4F). While the asynchronous limit cycle deeply differs from the synchronous one in terms of spatial synchrony, it shows identical mean regional densities at low dispersal rates. But when dispersal rates increase, prey regional density slowly decreases while predator regional density increases. These changes in mean regional densities are not accompanied with chaotic dynamics.

Moreover, these mean regional densities can be quantitatively affected by dispersal behaviours and relative dispersal: the mean regional density of the prey decreases and the mean regional density of the predator increases more strongly when $d_n > d_p$ and there is intraspecific density-dependent dispersal for the prey (only when $|x_{\alpha\beta}|=4$: fig. 3B; fig. 4B; $|x_{\alpha\beta}|=1$: Appendix B, fig. 5B,C) or interspecific density-dependent dispersal for the prey (fig. 3B; fig. 4B), or when $d_p > d_n$ and there is interspecific density-dependent dispersal for the predator (fig. 3F; fig. 4F). These changes commonly go hand in hand with the emergence of new chaotic regimes (fig. 3F; fig. 4F). As a consequence, density-dependent dispersal and relative dispersal can increase the strength of the impact of predator populations on prey populations at the regional scale, and thus increase the control of the predator on the prey.

Regional variability

The regional variability of prey and predator populations, as measured by the CV of their regional densities, may be strongly affected by density-dependent dispersal through both spatial synchrony and predator control on the prey. We should expect low regional variability when local dynamics are asynchronous and high regional variability when local dynamics are synchronous. Predator control on the prey should also affect the regional variability through changes in mean regional densities: this control should decrease predator regional variability and should increase prey regional variability.

When dispersal is constant, the regional variability of the prey and the predator is modified by their relative dispersal (fig. 3A, 3D; fig. 4A, 4D). When prey dispersal is higher than predator dispersal ($d_n > d_p$) (fig. 3A; fig. 4A), the regional variability of the prey and of the predator at low dispersal rates is slightly lower than their regional variability at high dispersal rate. This is caused by desynchronisation of dynamics at low dispersal rates for

both species (fig. 2A). But at intermediate dispersal rate, the regional variabilities of the prey and the predator vary in different way. Two mechanisms act in opposite direction for the prey and in the same direction for the predator. The increase in asynchrony tends to lower regional variability of both the prey and the predator, whereas predator control increases regional variability of the prey and decreases the predator's. As a result, the regional variability of the prey increases slightly while the predator's decreases strongly. When predator dispersal is higher than prey dispersal ($d_p > d_n$) (fig. 3D; fig. 4D), the regional variability of the prey and the predator can decrease when dispersal rates decrease. Indeed, at intermediate and low dispersal rates, two limit cycles coexist: the synchronous one has high regional variability and the asynchronous one shows low regional variability. Moreover, regional variability of the prey and the predator on this asynchronous limit cycle vary with increasing dispersal rates. The increase in asynchrony tends to lower regional variability of both the prey and the predator, whereas predator control increases regional variability of the prey and decrease the predator's. As a result, the regional variability of the prey increases slightly while the predator's decreases strongly. Thus, the effect of dispersal on a species regional variability depends on its trophic position.

When dispersal rates are high, as in a well-mixed system, the regional variabilities of the prey and the predator are not affected by the type of dispersal behaviour and by the relative dispersal. But when dispersal rates decrease, density-dependent dispersal can affect regional variabilities of both species, depending on their relative dispersal rates (fig. 3B, 3C, 3E, 3F; fig. 4B, 4C, 4E, 4F).

Density-dependent dispersal in the prey can modify regional variability when prey dispersal is higher than predator dispersal ($d_n > d_p$) (fig. 3B; fig. 4B). Intraspecific density-dependent dispersal in the prey can strongly modify regional variability of both species by comparison to constant dispersal. At intermediate dispersal rates, prey and predator regional variabilities vary in opposite way when $|x_{\alpha\beta}|=4$, because of the increase of spatial synchrony

(fig. 2B) and of predator control on the prey (fig. 3B; fig. 4B). Prey regional variability increases or decreases compared to constant dispersal, depending on the relative effects of these two mechanisms that act in opposite direction. On the contrary, these two mechanisms both decrease predator regional variability. At low dispersal rates, intraspecific density-dependent dispersal in the prey increases regional variability of both species because of spatial synchrony of periodic dynamics when $|x_{\alpha\beta}|=4$ and when $|x_{\alpha\beta}|=1$ (Appendix B, fig. 5B, C). The effects of interspecific density-dependent dispersal in the prey (fig. 3B; fig. 4B) on the relationship between dispersal rates and regional variability are qualitatively the same as under constant dispersal (fig. 3A; fig. 4A), but they are stronger. Indeed, prey and predator regional variabilities are strongly lower at low dispersal rates than at high dispersal rates because of strong spatial asynchrony at low dispersal rates. The transition between high and low dispersal rates occurs with increase of spatial asynchrony and of predator control on the prey. As a consequence, prey regional variability is increased whereas predator regional variability is decreased compared to constant dispersal.

Only interspecific density-dependent dispersal in the predator modifies regional variability when predator dispersal is higher than prey dispersal ($d_p > d_n$) (fig. 3C, 3F; fig. 4C, 4F). Intraspecific density-dependent dispersal in the predator does not affect prey and predator regional variability (fig. 3C, 3F; fig. 4C, 4F), which is consistent with the results on spatial dynamics and regional densities (fig. 2-4C, 2-4F). When predator dispersal depends on prey density, the synchronous limit cycle disappears at low and intermediate dispersal rates, leaving only the asynchronous limit cycle. As a consequence, prey and predator regional variabilities are strongly lower at low dispersal rates than at high dispersal rates, whatever the initial densities are. Moreover, between low and high dispersal rates, prey regional variability results of a balance between spatial synchrony and predator control on the prey, whereas these two mechanisms act in same way to decrease predator regional variability.

DISCUSSION

Our results when dispersal rates of the prey and the predator are constant, such as the potential coexistence of several attractors, are consistent with those obtained by Jansen (1995, 2001). They further show that density-dependent dispersal in both the prey and the predator and their relative dispersal rates may affect the nature of dynamics (periodic vs chaotic) and the spatial synchrony and stability of species when the symmetric equilibrium of the metacommunity is unstable and populations fluctuate over time.

Dispersal behaviours and spatial synchrony

One important factor that affects metacommunity stability is the spatial synchrony of the population dynamics of the various species. Since a species is more vulnerable to extinction when all its population densities in a metacommunity are low at the same time, spatial synchrony decreases the probability of persistence of that species at the regional scale (Briggs and Hoopes 2004). Spatial synchrony in predator-prey metacommunities is a balance between synchronising and desynchronising processes. Processes that desynchronise dynamics include different forms of stochasticity (Taylor 1990), but also nonlinear trophic interactions (Bjornstad 2000; de Roos *et al*. 1991; Jansen 1999). Local dynamics may be synchronised by environmental forcing (the "Moran" effect), high dispersal rates (Bjornstad *et al*. 1999, Vasseur and Fox 2009) and nonlinear trophic interactions when dispersal rates are low, (Bjornstad 2000; de Roos *et al*. 1991; Jansen 1999).

Our results show that density-dependent dispersal behaviours can affect spatial synchrony in metacommunities at low and intermediate dispersal rates. In particular, interspecific density-dependent dispersal can strongly desynchronise dynamics. In a patchy

Rosenzweig-MacArthur model, Li *et al*. (2005) observed the same trend when prey migration was negatively correlated to the gradient of predator density or when predator migration followed the gradient of prey density. However, their study was focused on equal dispersal rates in the prey and the predator. Here, we show that this effect depends on the relative dispersal of the two species: interspecific density-dependent dispersal in the prey has a strong impact when prey dispersal is higher than predator dispersal, whereas interspecific density-dependent in the predator has a strong impact when predator dispersal is higher than prey dispersal.

According Briggs and Hoopes (2004), spatial asynchrony in predator-prey metacommunities is increased when local population dynamics are uncoupled from immigration, i.e. when a local population receive more individuals when its density is low than when its density is high. Because prey and predator densities do not fluctuate synchronously within patches (predator abundance peaks after prey abundance), the dependence of a species' dispersal on the density of another species (interspecific density-dependent dispersal) could promote their uncoupling and increase spatial asynchrony.

We fund a stabilising effect of interspecific density-dependent dispersal in a patchy Rosenzweig-MacArthur model with identical patches in agreement with Li *et al*.'s results (2005) obtained in a similar model. By contrast, in patchy models with consistent differences between patches in parameter values and local dynamics that obey either the Lotka-Volterra model (Murdoch *et al*. 1992) or a variant with a type-II functional response (Ives 1992), the aggregation of the predator in patches of high prey density can be either synchronising or desynchronising. The desynchronising effect could come either from the absence of density-dependence in the prey growth rate (e.g. logistic growth), which is stabilising, or from the differences between patches.

Our results show also that the synchrony of spatial dynamics is affected by intraspecific density-dependent dispersal in the prey. This dispersal behaviour can fully

synchronise population dynamics at low dispersal rates, but can also desynchronise local dynamics at intermediate dispersal rates when the shape of density-dependence in dispersal is sigmoidal. Synchronising and desynchronising effects have been observed also in single-species metapopulation models (Ylikarjula *et al*. 2000). In our metacommunity model, we observed this effect for the prey, but not for the predator. We show that the effects of intraspecific density-dependent dispersal in the prey depend on relative dispersal: these effects are strong when prey dispersal is higher than predator dispersal. Thus, density-dependent dispersal and relative dispersal have interacting effects and play an important part in regulating spatial synchrony in metacommunities.

The interaction between density-dependent dispersal and relative dispersal suggests that density-dependent dispersal behaviours can have different effects on stability in different types of predator-prey systems. Predators often disperse more than their prey (Rooney *et al*. 2008). In such systems, our results suggest that interspecific density-dependent dispersal in the predator can modify stability whereas density-dependent dispersal in the prey does not. But prey sometimes disperse more than their predators (Rooney *et al*. 2008). In such situations, density-dependent dispersal in the prey can have a strong effect on the stability of the metacommunity: interspecific density-dependent dispersal can increase spatial synchrony, whereas intraspecific density-dependent dispersal can either decrease or increase it depending on dispersal rates.

Dispersal behaviours and top-down control

The extent to which populations are regulated by predation ("top-down" control) or by the availability of resources ("bottom-up" control) has been intensely debated in ecology (e.g. Hairston *et al*. 1960; Murdoch 1966; Oksanen *et al*. 1981). Most ecologists now agree that both types of control are present in most ecosystems (Shurin *et al*. 2002; Borer *et al*.

2005) and that their relative strength depends on local factors such as functional diversity (Hulot *et al.* 2000) and coevolution between prey and predators (Loeuille and Loreau 2004). Spatial processes can also modify the strength of these controls. A recent model predicts that nutrient inputs and immigration should generally increase the strength of trophic cascades in open ecosystems (Leroux and Loreau 2008).

Moreover, predator-prey metacommunity models reveal that dispersal between local communities can also modify the strength of top-down control. Stochastic predator-prey metacommunity models have shown that the relative abundances of the prey and the predator vary with dispersal rate: the mean of prey abundance decreases and the mean of predator abundance increases at intermediate dispersal rates (e.g. Reeve 1988; Zeigler 1977). We fund this result in our deterministic predator-prey model. It is based on a type-II functional response, which implies that the predator controls the prey at equilibrium. When prey and predator local densities fluctuate over time, we fund that the temporal mean of prey density decreases while the temporal mean of predator density increases at intermediate dispersal rates. These variations are observed both at the regional scale (fig. 3-4) and at the local scale (results not shown). Thus, results of our deterministic model and of stochastic models suggest that intermediate dispersal rates increase the average strength of the control of the prey by the predator in predator-prey metacommunities. Moreover our results show that intra- and interspecific density-dependent dispersal in the prey.reinforces the increase in the strength of predator control on the prey at intermediate dispersal rates.

The effect of dispersal on the strength of top-down control has some experimental support. In aquatic predator-prey metacommunities, the mean density of the predator (*Didinium nasutum*) was highest at intermediate dispersal rates whereas the mean density of the prey (*Colpidium striatum*) was decreased by dispersal (Holyoak and Lawler 1996b). In trophically more complex metacommunities, dispersal between mesocosms increased predator biomass, decreased herbivore biomass and increased primary producer biomass

(Chase *et al*. 2010). This suggests that the trophic cascade was stronger in mesocosms connected by dispersal than in isolated mesocosms. Thus, theory and experiments concur to suggest that dispersal and other spatial flows across ecosystems (Leroux and Loreau 2008) generally tend to increase the strength of top-down control food-web metacommunities.

Dispersal behaviours and the stability of metacommunities

Our results show that the synchrony of the prey and the predator are strongly related in metacommunities. Indeed, spatial synchrony is affected in the same way in the prey and in the predator by density-dependent dispersal and relative dispersal. In particular, density-dependent dispersal in a species can modify not only its own spatial synchrony, as in metapopulation models, but also the spatial synchrony of the other species. For instance, interspecific density-dependent dispersal in the prey can increase both its spatial asynchrony and that of the predator.

Metacommunity stability depends not only on spatial asynchrony but also on the strength of prey control by the predator: as discussed above, density-dependent dispersal increases predator control on the prey at intermediate dispersal rates. This generates a decrease in regional variability of the predator, and an increase in that of the prey. Regional persistence shows the same trends: the regional persistence of the predator is increased while that of the prey is decreased, although the latter effect is smaller than for regional variability (See supplementary material, fig. S3 and S4). Thus, the stability of the prey and that of the predator display opposite responses to density-dependent dispersal because of the increase in the average strength of predator control on the prey.

Although the regional stability (as measured by both persistence and variability) of the predator is maximal at intermediate dispersal rates, it is nevertheless lower than that of the prey. Thus, top-down control stabilises the less stable species (the predator) and

destabilises the more stable species (the prey). This suggests that the metacommunity as a whole may be stabilised at intermediate dispersal. This conclusion is consistent with the general finding of models including different forms of stochasticity that the persistence of predator-prey metacommunities is enhanced at intermediate dispersal rates (Crowley 1981; Reeve 1988; Zeigler 1977). The mechanism that is generally thought to generate the hump-shaped relationship between the stability of predator-prey metacommunities and dispersal is the balance between the positive effect of low dispersal (allowing recolonization and rescue effects) and the negative effect of high dispersal (synchronisation). Here we suggest that another mechanism could stabilise predator-prey metacommunities at intermediate dispersal rates: the modification of the strength of top-down control, which increases the stability of the most unstable species (the predator).

Our numerical results show a hump-shaped relationship between predator stability and dispersal for both constant and density-dependent dispersal. But they suggest that the hump can become more or less marked when dispersal is density dependent. For instance, the hump is stronger when the prey has intraspecific density-dependent dispersal because the latter destabilises the metacommunity at low dispersal rates (spatial synchronisation) and increases the stability at intermediate dispersal rates (strengthening of predator control on the prey). Although interspecific density-dependent dispersal in the prey stabilises the metacommunity at low dispersal (desynchronisation of local dynamics), the increase in the strength of predator control is sufficient to maintain the hump-shaped relationship between predator stability and dispersal.

Thus, density-dependent dispersal can modify the stability of predator-prey metacommunities by modifying both the spatial synchrony of local populations and the strength of prey control by the predator. We hope that these results will stimulate further work on the effects of dispersal on top-down control and the stability of food-web metacommunities.

Ecosystem fragmentation and conservation management

Ecosystem fragmentation leads to decreased species dispersal between patches. Therefore studying the relationship between dispersal and metacommunity stability is of particular importance to understand the response of metacommunities to fragmentation. We showed that this response may depend on the existence of density-dependent dispersal in species and on their relative dispersal. If fragmentation decreases dispersal of only one species in the metacommunity because of its specific sensitivity to changes in environmental quality between patches, relative dispersal will be modified. In the case of constant prey dispersal and interspecific density-dependent dispersal for the predator, for instance, our model predicts that decreased predator dispersal only may lead to destabilisation of the metacommunity. Thus our work emphasizes the importance of density-dependent dispersal and relative dispersal of species in understanding the response of ecosystems to fragmentation.

This also suggests that enhancing the dispersal of one species through e.g. corridors may not be the best way to prevent its own extinction. For instance, if prey dispersal is constant and predator dispersal is lower and depends on prey density, the increase in prey dispersal by corridors will not increase its stability. In contrast, an increase in predator dispersal may stabilise both the prey and the predator if the ratio between the dispersal rates of the two species is reversed. Thus, our results emphasize the need to integrate conservation policies at the scale of communities and metacommunities, instead of considering them merely at the scale of populations and metapopulations.

CONCLUSION

Our work shows that density-dependent dispersal, which generates interactions between local and regional dynamics, and relative dispersal of the prey and the predator are key to understand the dynamics and stability of metacommunities. Density-dependent dispersal behaviours and relative dispersal deserve more theoretical and experimental explorations to increase our ability to predict the effects of habitat fragmentation on the stability of ecosystems.

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APPENDIX A: STABILITY ANALYSIS OF SYMMETRICAL EQUILIBRIUM

Linearization of two-patch model with density-dependent dispersal

We used the method proposed by Jansen (1994) and generalised it to density-dependent dispersal. System of equations (1), and more generally a two-patch model of predator-prey dynamics, can be written in vectorial form into:

$$\begin{cases} \dfrac{dX}{dt} = F(X) - G(X) + G(Y) \\ \dfrac{dY}{dt} = F(Y) - G(Y) + G(X) \end{cases} \qquad (2)$$

where $X = \begin{pmatrix} N_1 \\ P_1 \end{pmatrix}$ and $Y = \begin{pmatrix} N_2 \\ P_2 \end{pmatrix}$ are the vectors of population densities of the prey (N) and of the predator (P) in patches 1 and 2. The local dynamics of the prey and the predator are described by the functions $F(X) = \begin{pmatrix} f_N(X) \\ f_P(X) \end{pmatrix}$ and $F(Y) = \begin{pmatrix} f_N(Y) \\ f_P(Y) \end{pmatrix}$. The dispersal dynamics of both species in patch 1 and 2 are described respectively by the functions $G(X) = \begin{pmatrix} g_N(X) \\ g_P(X) \end{pmatrix}$ and $G(Y) = \begin{pmatrix} g_N(Y) \\ g_P(Y) \end{pmatrix}$.

The symmetric equilibrium of (2), noted (X^*, Y^*) is those for which $X(t)=Y(t)$ for all t. In order to facilitate the analysis of symmetric equilibrium, we introduce $\Sigma = \frac{1}{2}(X+Y) = \begin{pmatrix} \Sigma_N \\ \Sigma_P \end{pmatrix}$, the vector of average densities of each species over the two patches, and $\Delta = X - \Sigma = \Sigma - Y = \frac{1}{2}(X-Y) = \begin{pmatrix} \Delta_N \\ \Delta_P \end{pmatrix}$, the vector of differences between densities in a patch and average densities in the metacommunity.

System (2) can then be recast into:

$$\begin{cases} \dfrac{d\Sigma}{dt} = \dfrac{1}{2}\left[F(\Sigma+\Delta)+F(\Sigma-\Delta)\right] \\ \dfrac{d\Delta}{dt} = \dfrac{1}{2}\left[F(\Sigma+\Delta)-F(\Sigma-\Delta)\right]-G(\Sigma+\Delta)+G(\Sigma-\Delta) \end{cases} \quad (3)$$

We are interested in the equilibrium (Σ^*, Δ^*) of (3) and more particularly to the symmetric equilibria (Σ^*, $\Delta^*=0$). Note that for $\Delta = 0$, the dynamics of the mean densities, Σ, is exactly the same as the local dynamics of densities in the absence of migration. In particular, the equilibrium values of Σ are the equilibrium values of the local dynamics determined by F. In order to study the stability near a symmetric equilibrium, the system (3) is linearized around $\Sigma = \Sigma^*$, $\Delta = 0$:

$$\begin{cases} \dfrac{d\Sigma}{dt} = \boldsymbol{J}_F(\Sigma^*)\times(\Sigma-\Sigma^*)+o\left(\left\|\Sigma-\Sigma^*\right\|+\left\|\Delta\right\|\right) & (4.1) \\ \dfrac{d\Delta}{dt} = \left[\boldsymbol{J}_F(\Sigma^*)-2\boldsymbol{J}_G(\Sigma^*)\right]\times\Delta+o\left(\left\|\Sigma-\Sigma^*\right\|+\left\|\Delta\right\|\right) & (4.2) \end{cases}$$

where $\boldsymbol{J}_F(\Sigma^*)=\left.\begin{pmatrix} \dfrac{\partial f_N}{\partial N} & \dfrac{\partial f_N}{\partial P} \\ \dfrac{\partial f_P}{\partial N} & \dfrac{\partial f_P}{\partial P} \end{pmatrix}\right|_{\substack{N=\Sigma_N^* \\ P=\Sigma_P^*}}$ and $\boldsymbol{J}_G(\Sigma^*)=\left.\begin{pmatrix} \dfrac{\partial g_N}{\partial N} & \dfrac{\partial g_N}{\partial P} \\ \dfrac{\partial g_P}{\partial N} & \dfrac{\partial g_P}{\partial P} \end{pmatrix}\right|_{\substack{N=\Sigma_N^* \\ P=\Sigma_P^*}}$ are the Jacobian matrices of F and G.

The stability of ($\Sigma = \Sigma^*$, $\Delta = 0$) is determined by the eigenvalues of matrices $J_F(\Sigma^*)$ and $J_F(\Sigma^*)-2\,J_G(\Sigma^*)$. The equilibrium ($\Sigma = \Sigma^*$, $\Delta = 0$) of system (4), or the symmetrical equilibrium (X^*, Y^*) of system (2), is stable if both matrices $J_F(\Sigma^*)$ and $J_F(\Sigma^*)-2\,J_G(\Sigma^*)$ do not have eigenvalues with positive real part. Since these matrices are of dimension 2, this is equivalent to:

$$\begin{cases} Tr\left(\boldsymbol{J}_F(\Sigma^*)\right)<0 \\ \det\left(\boldsymbol{J}_F(\Sigma^*)\right)>0 \end{cases} \text{ and } \begin{cases} Tr\left(\boldsymbol{J}_F(\Sigma^*)-2\,\boldsymbol{J}_G(\Sigma^*)\right)<0 \\ \det\left(\boldsymbol{J}_F(\Sigma^*)-2\,\boldsymbol{J}_G(\Sigma^*)\right)>0 \end{cases}$$

Application to the two-patch Rosenzweig – MacArthur model

In order to determine the effects of density-dependent dispersal on the stability of the symmetric equilibrium of (1), we analyse the signs of the trace and of the determinant of the matrices $J_F(\Sigma^*)$ and $J_F(\Sigma^*) - 2\ J_G(\Sigma^*)$, where *F* and *G* correspond to our specific model.

In our specific model, *F* and *G* write:

$$F(N,P) = \begin{pmatrix} r\,N\left(1-\frac{N}{K}\right) - \frac{b\,N\,P}{c+N} \\ \frac{b\,N\,P}{c+N} - m\,P \end{pmatrix} \text{ and } G(N,P) = \begin{pmatrix} N\,D_N(N,P) \\ P\,D_P(N,P) \end{pmatrix}$$

, where D_N and D_P are the *per capita* dispersal rate of the prey and the predator. We allow any form of density-dependant dispersal rates, provided that prey dispersal increases with prey density ($\partial D_N/\partial N > 0$) and predator density ($\partial D_N/\partial P > 0$) and that predator dispersal increases with predator density ($\partial D_P/\partial P > 0$) and decreases with prey density ($\partial D_P/\partial N < 0$).Thus, the sign structure of the Jacobian matrix of *F* and *G* at Σ* are:

$$\boldsymbol{J}_F(\Sigma^*) = \begin{pmatrix} * & - \\ + & 0 \end{pmatrix} \text{ and } \boldsymbol{J}_G(\Sigma^*) = \begin{pmatrix} + & + \\ - & + \end{pmatrix}$$

, where * is determined by the sign of $K - c(b+m)/(b-m)$. The determinant of $J_F(\Sigma^*)$ is positive and its trace is equal to the * term. The *term is negative, and thus Σ* is a stable equilibrium of (4.1) if and only if $K < c(b+m)/(b-m)$. At the transition, both eigenvalues real parts vanish, which indicates a (here supercritical) Hopf bifurcation. When *K* passes the threshold value $c(b+m)/(b-m)$, the equilibrium becomes unstable and dynamics converges to a stable limit cycle.

Given * term is negative, the sign structure of J_G implies that $J_F(\Sigma^*) - 2\ J_G(\Sigma^*)$ has a stable sign structure: when $K < c(b+m)/(b-m)$, the trace of $J_F(\Sigma^*) - 2\ J_G(\Sigma^*)$ is

negative and its determinant is positive. As a consequence, when $K < c(b+m)/(b-m)$, the solution $\Delta^* = 0$ of (4.2) is a stable equilibrium.

Thus, the stability condition for the non-spatial Rosenzweig – MacArthur model carries over to the symmetric equilibrium of the spatial model, whatever the dispersal behaviours.

APPENDIX B: SENSITIVITY TO SHAPE OF DENSITY DEPENDENCE IN DISPERSAL

(fig. 5)

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LEGENDS OF FIGURES

Figure 1. *Per capita* dispersal rate D_α of species α ($\alpha = n$ or $\alpha = p$) in response to changes in the density of species β ($\beta = n$ or $\beta = p$). $S_{\alpha\beta}$ is the half-saturation parameters. Density-independent ($x_{\alpha\beta}$=0: solid line) dispersal; positive (black dashed line) and negative (grey dashed line) density-dependent dispersal; cyrtoid ($|x_{\alpha\beta}|$=1: thin dashed lines) and sigmoid ($|x_{\alpha\beta}|$=4: thick dashed lines) shape of density dependence in dispersal.

Figure 2. Dynamics and spatial synchrony of the prey in predator-prey metacommunities as functions of its maximal dispersal rate (d_n). Top diagrams illustrate the various cases studied: N and P represent prey and predator densities; dispersal of each species is represented by a wide white arrow; positive or negative effects of densities on dispersal are represented by thin solid arrows with a + or a - sign. Figures in the first column (A and D) present results when dispersal is constant in both species. In the second column (B and E), we present results for (intra- and interspecific) density-dependent dispersal in the prey. In the third column (C and F), we present results for (intra- and interspecific) density-dependent dispersal in the predator. We present results for $d_n = 100\ d_p$ ($d_n > d_p$) and for $d_p = 100\ d_n$ ($d_p > d_n$) in the first (A,B and C), and in the second (D, E and F) row, respectively. Markers on curves (except for A and D) indicate what type of density dependence the curve refers to: intraspecific (dots) or interspecific (triangles). The nature of dynamics obtained using the Lyapunov exponent is represented on curves: chaotic dynamics (with colour thickening) or periodic dynamics (without colour thickening). The specific colours used (gray, cyan and red) as well as the position of the thickening (above or under the curve) only help, in addition to curve markers, to distinguish between the different curves and do not have any further meaning. Notice on figures D, E, F ($d_p > d_n$) the two coexisting attractors (synchronous and asynchronous) for some dispersal rate values. Parameters values are the following. Constant dispersal: $x_{\alpha\beta}$=0; positive density-dependent dispersal: $x_{\alpha\beta}$=4 ($\alpha\beta$=*nn*,*np*,*pp*); negative density-dependent dispersal: x_{pn}=-4. Other parameters: S_{nn}=18, S_{np}=2, S_{pp}=2, S_{pn}=18; local interactions: r=10, K=25, b=11, c=1, m=10.

Figure 3.Temporal mean of regional density (upper sub-graph) and coefficient of variation (CV, lower sub-graph) of the prey in predator-prey metacommunities as functions of its maximal dispersal rate (d_n). See legend of figure 2.

Figure 4. Temporal mean of regional density (upper sub-graph) and coefficient of variation (CV, lower sub-graph) of the predator in predator-prey metacommunities as functions of the maximal dispersal rate of the prey (d_n). See legend of figure 2.

Figure 5. The effect of intraspecific density-dependent dispersal in the prey when x_{nn}=1. The spatial synchrony (A), the temporal mean of regional densities (upper sub graph) and the coefficient of variation (CV, lower sub graph) of the prey (B) and of the predator (C) as functions of the maximal dispersal rate of the prey (d_n). We present results for $d_n = 100\ d_p$ ($d_n > d_p$). The curve coding is the same as in figure 2. Notice that, compared to figures 2, 3 and 4, intraspecific density-dependent dispersal does not induce chaotic dynamics any more and that two attractors can now coexist at intermediate dispersal rates. Parameters values are the same as in figure 2, except $|x_{nn}|$=1.