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Density-dependent dispersal and relative dispersal affect the stability of predator-prey metacommunities

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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

1 INTRODUCTION

2
3 Understanding the mechanisms that govern the stability of metacommunities is a key
4 challenge to understand the response of ecosystems to fragmentation. Metacommunities are
5 regional sets of local communities linked by dispersal, i.e., by the movement of individuals
6 from a patch (emigration) to another (immigration) (Leibold *et al.* 2004). Both local and
7 regional processes affect the stability of metacommunities. For instance, in predator-prey
8 metacommunities, local processes such as local density regulation mechanisms drive local
9 predator-prey population fluctuations, which may lead to local extinctions when
10 communities are isolated (Gause 1934; Lotka 1925; Rosenzweig and MacArthur 1963;
11 Volterra 1926). But dispersal, which is a regional process, may allow regional persistence of
12 the prey and the predator (Huffaker 1958) because it allows recolonization of vacant patches
13 (Levins 1970) or rescue effects (Brown and Kodric-Brown 1977). This positive effect of
14 dispersal on the regional stability of predator-prey metacommunities requires that dynamics
15 are spatially asynchronous. If local populations fluctuate strongly and synchronously, the
16 whole metapopulation may go extinct because of simultaneous extinction of local
17 populations. But if fluctuations of local densities are asynchronous, recolonizations or
18 rescue effects can occur and the persistence and stability of the metacommunity is improved
19 (Comins and Blatt 1974; Hassell *et al.* 1991; Jansen 2001).

20
21 But dispersal and synchrony between communities are not independent processes.
22 On the one hand, dispersal may increase spatial synchrony because exchanges of individuals
23 between communities tend to reduce differences in population sizes, especially when
24 dispersal is high (Bjornstad *et al.* 1999). On the other hand, weak dispersal may also
25 synchronise dynamics in predator-prey metacommunities with nonlinear density regulation
26 (Bjornstad 2000; Jansen 1999). Thus, both dispersal and local density regulation can

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

21
22 In this paper, we investigate the influence of two key aspects of dispersal behaviours
23 on the stability of predator-prey metacommunities: the density dependence in dispersal, and
24 the ratio of predator and prey dispersal rates, which we name "relative dispersal". Density-
25 dependent dispersal, i.e. dispersal changes in response to changes of species densities in the
26 donor patch, has been observed in several experimental systems (see for instance Bernstein

1 1984; French and Travis 2001; Hauzy *et al.* 2007). It implies a direct effect of local
2 processes (population dynamics) on regional processes (dispersal). A species' population
3 density can affect its own dispersal (intraspecific density-dependent dispersal) or the
4 dispersal of another species (interspecific density-dependent dispersal). Recent models
5 including density-dependent dispersal in predator-prey metacommunities yielded contrasted
6 results. McCann *et al.* (2000) suggested that local predator population outbreaks do not
7 depend on interspecific density-dependent dispersal. By contrast, Li *et al.* (2005) showed
8 that interspecific density-dependent dispersal can reduce spatial synchrony in both the prey
9 and the predator. Most of these studies, however, have assumed that prey and predator
10 dispersal rates are equal. But empirical data suggest that dispersal abilities of prey and
11 predator can be very different. The large range of predator-prey body-size ratios observed in
12 real food webs (Brose *et al.* 2006) and the allometric relationship between body size and the
13 scale of species' movements (Rooney *et al.* 2008) or dispersal abilities (Jenkins *et al.* 2007)
14 suggest that the relative dispersal rate of the predator compared to the prey can vary within a
15 large range. In some ecosystems, scale of movement is strongly positively related to trophic
16 position, suggesting a higher dispersal rate for the predator than for the prey. In other
17 systems, predators can even be less mobile than their prey, suggesting a higher dispersal rate
18 for the prey than for the predator. Differences in the dispersal abilities of the prey and the
19 predator can have important consequences, and yet have received little attention so far.

20
21 Here we develop a deterministic metacommunity model of a prey and a predator that
22 includes density-dependent dispersal. We compare the effects of both intra- and
23 interspecific density-dependent dispersal on the dynamics and the stability of the prey and
24 the predator at the regional scale with those of constant dispersal. We study the effects of
25 density-dependent dispersal in two contrasting cases of relative dispersal: either predator
26 dispersal is distinctly higher than prey dispersal or prey dispersal is distinctly higher than

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

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1 **THE MODEL**

2

3 We consider a patchy landscape consisting of several localities. Each locality is
 4 occupied by a local predator-prey community. Within each community, local dynamics
 5 follow a Rosenzweig–MacArthur predator-prey model (Rosenzweig and MacArthur 1963):
 6 prey growth is logistic, the predator has a Holling type II functional response and its
 7 mortality rate is constant. Local communities are linked by dispersal of both species from
 8 one patch to another. A collection of such communities constitutes a predator-prey
 9 metacommunity. For the sake of simplicity, and following Jansen (1995, 2001), we study a
 10 2-patch predator-prey metacommunity in which the two patches are identical. The dynamics
 11 of the prey and the predator in the two patches (1 and 2) are given by a system of ordinary
 12 differential equations:

13

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

15

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

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

3

4 The last two terms of equations describe dispersal from and to each patch. We make
 5 the ecological hypothesis that migration is not costly; as a consequence, the emigration term
 6 in one patch corresponds exactly to the immigration term in the other. This assumption fits
 7 in well with dispersal through corridors that allow fast moves with limited mortality risks.

8 Dispersal rates are determined locally: the *per capita* dispersal rates from patch i of the prey
 9 $D_n(N_i, P_i)$ and of the predator $D_p(N_i, P_i)$ are functions of species densities in the donor patch
 10 i only. The dispersal rate of each species may depend on its own local density, which we
 11 refer to as "intraspecific density-dependent dispersal", and on the local density of the other
 12 species, which we refer to as "interspecific density-dependent dispersal" (Hauzy *et al.*

13 2007). Our mathematical analysis deals with the general model, but our numerical
 14 simulations investigate the separate effects of intraspecific and interspecific density
 15 dependence in dispersal. The dispersal rates then simplify into $D_n(N_i)$ or $D_n(P_i)$ and $D_p(P_i)$
 16 or $D_p(N_i)$. In numerical simulations, density dependence in dispersal is modelled through
 17 Hill functions, which have been chosen for their convenient plasticity: the *per capita*
 18 dispersal rate from patch i of the prey writes

$$19 \quad D_n(N_i) = d_n \frac{N_i^{x_{nm}}}{S_{nm}^{x_{nm}} + N_i^{x_{nm}}} \quad \text{or} \quad D_n(P_i) = d_n \frac{P_i^{x_{np}}}{S_{np}^{x_{np}} + P_i^{x_{np}}}$$

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

$$21 \quad D_p(P_i) = d_p \frac{P_i^{x_{pp}}}{S_{pp}^{x_{pp}} + P_i^{x_{pp}}} \quad \text{or} \quad D_p(N_i) = d_p \frac{N_i^{x_{pn}}}{S_{pn}^{x_{pn}} + N_i^{x_{pn}}}.$$

22

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

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

13

14 In this paper, we explore density-dependent dispersal behaviours that mimic those
 15 observed in several experiments (Bernstein 1984; French and Travis 2001; Hauzy *et al.*
 16 2007), i.e., prey dispersal increases with prey and predator densities (positive intra- and
 17 interspecific density-dependent dispersal in the prey), and predator dispersal increases with
 18 predator density (positive intraspecific density-dependent dispersal in the predator) and
 19 decreases with prey density (negative interspecific density-dependent dispersal in the
 20 predator). In terms of model parameters, this implies $x_{nn} > 0$, $x_{np} > 0$, $x_{pp} > 0$ and $x_{pn} < 0$. We
 21 conduct both a mathematical and a numerical analysis of the model.

22

23

1 MATHEMATICAL ANALYSIS

2

3 *Stability of the symmetric equilibrium*

4

5 We first focus on equilibriums of the model, and more specifically on the symmetric
6 equilibrium, i.e., that for which densities are equal in patches 1 and 2 ($N_1=N_2$ and $P_1=P_2$).

7 We analyse the stability of this equilibrium using the linearization method developed by
8 Jansen (1994). The original method considers a predator-prey metacommunity model with
9 constant dispersal. We extend the method to general forms of density-dependent dispersal
10 and apply it to our model (Appendix A).

11

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

22

23 *Regional densities at the symmetric equilibrium*

24

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

12

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1 NUMERICAL ANALYSIS

2
3 When $K > c(b+m)/(b-m)$, There is no stable equilibrium any longer, and the prey
4 and the predator show persistent oscillations through time. We used numerical simulations
5 to investigate the effect of density-dependent dispersal on prey and predator asymptotic
6 dynamics at the scale of the metacommunity.

7 8 *Methods*

9
10 We studied the various types of dispersal separately, *i.e.*, we studied constant
11 dispersal in both species, intraspecific density-dependent dispersal in either the prey or the
12 predator, and interspecific density-dependent dispersal in either the prey or the predator. For
13 each of these five types of dispersal, we also studied two contrasting relative dispersal rates,
14 one in which the maximal dispersal rate of the predator, d_p , is lower than that of the prey, d_n
15 ($d_p = 0.01 d_n$) and one in which the converse is true ($d_p = 100 d_n$). Maximal dispersal rates
16 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
17 these ranges, we took 1000 sample values of each parameter (keeping the ratio d_n/d_p
18 constant), uniformly distributed on a log scale. The parameters of local interactions were the
19 following: $r=10$, $K=25$, $b=11$, $c=1$, $m=10$. For the density dependence in dispersal, we
20 focused the numerical analysis on sigmoidal shapes ($|x_{\alpha\beta}|=4$, $\alpha=n,p$; $\beta=n,p$) and on values
21 for the half-saturation parameters $S_{\alpha\beta}$ set close to the mean densities observed when
22 populations are isolated: $S_{nn}=S_{pn}=18$ and $S_{np}=S_{pp}=2$.

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

1 asymptotic regime. This "asymptotic time" (t_{asympt}) was much wider for low dispersal rates;
2 it was then to 2×10^4 time units for high dispersal rates ($\text{Min}(d_n, d_p) > 10^{-4}$) and 2×10^5
3 time units for low dispersal rates ($\text{Min}(d_n, d_p) < 10^{-4}$). Our results were obtained from
4 population dynamics observed between t_{asympt} and $t_{\text{asympt}} + 10^4$, except for the first Lyapunov
5 exponent (see below), which was calculated on dynamics between $t_{\text{asympt}} + 10^4$ and $t_{\text{asympt}} +$
6 $2 \cdot 10^4$.

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

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

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

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

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

16 In order to investigate the robustness of our results with regard to changes in
17 dispersal parameters, we used a factorial design in which the independent variables were the
18 shape of the density dependence of the dispersal rates ($|x_{\alpha\beta}|$), their half-saturation parameters
19 ($S_{\alpha\beta}$), and their maximal values for both the prey and the predator (d_n and d_p). We compared
20 two different shapes, cyrtoid ($|x_{\alpha\beta}|=1$) and sigmoid ($|x_{\alpha\beta}|=4$). We varied the half-saturation
21 parameters $S_{\alpha\beta}$ by 20% above and below the mean densities when population are isolated
22 ($S_{nn}=S_{pn}=18$ and $S_{np}=S_{pp}=2$). We also varied the maximal dispersal rates of the prey (d_n) and
23 the predator (d_p) between 10^{-6} and 10^2 . Within this range, we took a sample of 100 values
24 for each parameter d_n and d_p (and up to 200 values for the reference parameter combination
25 $|x_{\alpha\beta}|=4$, $S_{nn}=S_{pn}=18$ and $S_{np}=S_{pp}=2$), uniformly distributed on a log scale (see supplementary
26 material, fig. S1 and S2).

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Metacommunity dynamics

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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

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

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

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

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

9

10 *Regional densities*

11

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

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

17 When dispersal rates are high, as in a well-mixed system, the regional variabilities of
18 the prey and the predator are not affected by the type of dispersal behaviour and by the
19 relative dispersal. But when dispersal rates decrease, density-dependent dispersal can affect
20 regional variabilities of both species, depending on their relative dispersal rates (fig. 3B, 3C,
21 3E, 3F; fig. 4B, 4C, 4E, 4F).

22 Density-dependent dispersal in the prey can modify regional variability when prey
23 dispersal is higher than predator dispersal ($d_n > d_p$) (fig. 3B; fig. 4B). Intraspecific density-
24 dependent dispersal in the prey can strongly modify regional variability of both species by
25 comparison to constant dispersal. At intermediate dispersal rates, prey and predator regional
26 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.

1 DISCUSSION

2

3 Our results when dispersal rates of the prey and the predator are constant, such as the
4 potential coexistence of several attractors, are consistent with those obtained by Jansen
5 (1995, 2001). They further show that density-dependent dispersal in both the prey and the
6 predator and their relative dispersal rates may affect the nature of dynamics (periodic vs
7 chaotic) and the spatial synchrony and stability of species when the symmetric equilibrium
8 of the metacommunity is unstable and populations fluctuate over time.

9

10 *Dispersal behaviours and spatial synchrony*

11

12 One important factor that affects metacommunity stability is the spatial synchrony of
13 the population dynamics of the various species. Since a species is more vulnerable to
14 extinction when all its population densities in a metacommunity are low at the same time,
15 spatial synchrony decreases the probability of persistence of that species at the regional
16 scale (Briggs and Hoopes 2004). Spatial synchrony in predator-prey metacommunities is a
17 balance between synchronising and desynchronising processes. Processes that
18 desynchronise dynamics include different forms of stochasticity (Taylor 1990), but also
19 nonlinear trophic interactions (Bjornstad 2000; de Roos *et al.* 1991; Jansen 1999). Local
20 dynamics may be synchronised by environmental forcing (the "Moran" effect), high
21 dispersal rates (Bjornstad *et al.* 1999, Vasseur and Fox 2009) and nonlinear trophic
22 interactions when dispersal rates are low, (Bjornstad 2000; de Roos *et al.* 1991; Jansen
23 1999).

24

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

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

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

16 We find a stabilising effect of interspecific density-dependent dispersal in a patchy
17 Rosenzweig-MacArthur model with identical patches in agreement with Li *et al.*'s results
18 (2005) obtained in a similar model. By contrast, in patchy models with consistent
19 differences between patches in parameter values and local dynamics that obey either the
20 Lotka-Volterra model (Murdoch *et al.* 1992) or a variant with a type-II functional response
21 (Ives 1992), the aggregation of the predator in patches of high prey density can be either
22 synchronising or desynchronising. The desynchronising effect could come either from the
23 absence of density-dependence in the prey growth rate (e.g. logistic growth), which is
24 stabilising, or from the differences between patches.

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

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

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

21 *Dispersal behaviours and top-down control*

22
23 The extent to which populations are regulated by predation ("top-down" control) or
24 by the availability of resources ("bottom-up" control) has been intensely debated in ecology
25 (e.g. Hairston *et al.* 1960; Murdoch 1966; Oksanen *et al.* 1981). Most ecologists now agree
26 that both types of control are present in most ecosystems (Shurin *et al.* 2002; Borer *et al.*

1 2005) and that their relative strength depends on local factors such as functional diversity
2 (Hulot *et al.* 2000) and coevolution between prey and predators (Loeuille and Loreau 2004).
3 Spatial processes can also modify the strength of these controls. A recent model predicts
4 that nutrient inputs and immigration should generally increase the strength of trophic
5 cascades in open ecosystems (Leroux and Loreau 2008).

6 Moreover, predator-prey metacommunity models reveal that dispersal between local
7 communities can also modify the strength of top-down control. Stochastic predator-prey
8 metacommunity models have shown that the relative abundances of the prey and the
9 predator vary with dispersal rate: the mean of prey abundance decreases and the mean of
10 predator abundance increases at intermediate dispersal rates (e.g. Reeve 1988; Zeigler
11 1977). We found this result in our deterministic predator-prey model. It is based on a type-II
12 functional response, which implies that the predator controls the prey at equilibrium. When
13 prey and predator local densities fluctuate over time, we found that the temporal mean of
14 prey density decreases while the temporal mean of predator density increases at
15 intermediate dispersal rates. These variations are observed both at the regional scale (fig. 3-
16 4) and at the local scale (results not shown). Thus, results of our deterministic model and of
17 stochastic models suggest that intermediate dispersal rates increase the average strength of
18 the control of the prey by the predator in predator-prey metacommunities. Moreover our
19 results show that intra- and interspecific density-dependent dispersal in the prey reinforces
20 the increase in the strength of predator control on the prey at intermediate dispersal rates.

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

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

5
6 *Dispersal behaviours and the stability of metacommunities*
7

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

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

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

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

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

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

1

2

Ecosystem fragmentation and conservation management

3

4

Ecosystem fragmentation leads to decreased species dispersal between patches.

5

Therefore studying the relationship between dispersal and metacommunity stability is of

6

particular importance to understand the response of metacommunities to fragmentation. We

7

showed that this response may depend on the existence of density-dependent dispersal in

8

species and on their relative dispersal. If fragmentation decreases dispersal of only one

9

species in the metacommunity because of its specific sensitivity to changes in

10

environmental quality between patches, relative dispersal will be modified. In the case of

11

constant prey dispersal and interspecific density-dependent dispersal for the predator, for

12

instance, our model predicts that decreased predator dispersal only may lead to

13

destabilisation of the metacommunity. Thus our work emphasizes the importance of

14

density-dependent dispersal and relative dispersal of species in understanding the response

15

of ecosystems to fragmentation.

16

This also suggests that enhancing the dispersal of one species through e.g. corridors

17

may not be the best way to prevent its own extinction. For instance, if prey dispersal is

18

constant and predator dispersal is lower and depends on prey density, the increase in prey

19

dispersal by corridors will not increase its stability. In contrast, an increase in predator

20

dispersal may stabilise both the prey and the predator if the ratio between the dispersal rates

21

of the two species is reversed. Thus, our results emphasize the need to integrate

22

conservation policies at the scale of communities and metacommunities, instead of

23

considering them merely at the scale of populations and metapopulations.

24

25

1 CONCLUSION

2

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

9

10

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20

21

1 **APPENDIX A: STABILITY ANALYSIS OF SYMMETRICAL EQUILIBRIUM**

2 *Linearization of two-patch model with density-dependent dispersal*

3

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

7
$$\begin{cases} \frac{dX}{dt} = F(X) - G(X) + G(Y) \\ \frac{dY}{dt} = F(Y) - G(Y) + G(X) \end{cases} \quad (2)$$

8 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

9 (N) and of the predator (P) in patches 1 and 2. The local dynamics of the prey and the

10 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

11 dispersal dynamics of both species in patch 1 and 2 are described respectively by the

12 functions $G(X) = \begin{pmatrix} g_N(X) \\ g_P(X) \end{pmatrix}$ and $G(Y) = \begin{pmatrix} g_N(Y) \\ g_P(Y) \end{pmatrix}$.

13 The symmetric equilibrium of (2), noted (X^*, Y^*) is those for which $X(t)=Y(t)$ for all
14 t . In order to facilitate the analysis of symmetric equilibrium, we introduce

15 $\Sigma = \frac{1}{2}(X + Y) = \begin{pmatrix} \Sigma_N \\ \Sigma_P \end{pmatrix}$, the vector of average densities of each species over the two patches,

16 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

17 patch and average densities in the metacommunity.

18 System (2) can then be recast into:

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

We are interested in the equilibrium (Σ^*, Δ^*) of (3) and more particularly to the symmetric equilibria $(\Sigma^*, \Delta^*=0)$. 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 $\Sigma = \Sigma^*, \Delta = 0$:

$$\begin{cases} \frac{d\Sigma}{dt} = J_F(\Sigma^*) \times (\Sigma - \Sigma^*) + o(\|\Sigma - \Sigma^*\| + \|\Delta\|) \\ \frac{d\Delta}{dt} = [J_F(\Sigma^*) - 2J_G(\Sigma^*)] \times \Delta + o(\|\Sigma - \Sigma^*\| + \|\Delta\|) \end{cases} \quad (4.1) \quad (4.2)$$

where $J_F(\Sigma^*) = \begin{pmatrix} \frac{\partial f_N}{\partial N} & \frac{\partial f_N}{\partial P} \\ \frac{\partial f_P}{\partial N} & \frac{\partial f_P}{\partial P} \end{pmatrix}_{\substack{N=\Sigma_N^* \\ P=\Sigma_P^*}}$ and $J_G(\Sigma^*) = \begin{pmatrix} \frac{\partial g_N}{\partial N} & \frac{\partial g_N}{\partial P} \\ \frac{\partial g_P}{\partial N} & \frac{\partial g_P}{\partial P} \end{pmatrix}_{\substack{N=\Sigma_N^* \\ P=\Sigma_P^*}}$ 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 $J_F(\Sigma^*) - 2J_G(\Sigma^*)$. 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 $J_F(\Sigma^*) - 2J_G(\Sigma^*)$ do not have eigenvalues with positive real part. Since these matrices are of dimension 2, this is equivalent to:

$$\begin{cases} Tr(J_F(\Sigma^*)) < 0 \\ \det(J_F(\Sigma^*)) > 0 \end{cases} \quad \text{and} \quad \begin{cases} Tr(J_F(\Sigma^*) - 2J_G(\Sigma^*)) < 0 \\ \det(J_F(\Sigma^*) - 2J_G(\Sigma^*)) > 0 \end{cases}$$

17

1 *Application to the two-patch Rosenzweig – MacArthur model*

2

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

6 In our specific model, F and G write:

7
$$F(N, P) = \begin{pmatrix} rN \left(1 - \frac{N}{K}\right) - \frac{bNP}{c+N} \\ \frac{bNP}{c+N} - mP \end{pmatrix} \text{ and } G(N, P) = \begin{pmatrix} ND_N(N, P) \\ PD_P(N, P) \end{pmatrix}$$

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

13
$$J_F(\Sigma^*) = \begin{pmatrix} * & - \\ + & 0 \end{pmatrix} \text{ and } J_G(\Sigma^*) = \begin{pmatrix} + & + \\ - & + \end{pmatrix}$$

14 , where $*$ is determined by the sign of $K - c(b+m)/(b-m)$. The determinant of
15 $J_F(\Sigma^*)$ is positive and its trace is equal to the $*$ term. The $*$ term is negative, and thus Σ^* is a
16 stable equilibrium of (4.1) if and only if $K < c(b+m)/(b-m)$. At the transition, both
17 eigenvalues real parts vanish, which indicates a (here supercritical) Hopf bifurcation. When
18 K passes the threshold value $c(b+m)/(b-m)$, the equilibrium becomes unstable and
19 dynamics converges to a stable limit cycle.

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

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

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

6

7 **APPENDIX B: SENSITIVITY TO SHAPE OF DENSITY DEPENDENCE IN** 8 **DISPERSAL**

9 (fig. 5)

10

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6

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1 **LEGENDS OF FIGURES**

2
 3 Figure 1. *Per capita* dispersal rate D_α of species α ($\alpha = n$ or $\alpha = p$) in response to changes in
 4 the density of species β ($\beta = n$ or $\beta = p$). $S_{\alpha\beta}$ is the half-saturation parameters. Density-
 5 independent ($x_{\alpha\beta}=0$: solid line) dispersal; positive (black dashed line) and negative (grey
 6 dashed line) density-dependent dispersal; cyrtoid ($|x_{\alpha\beta}|=1$: thin dashed lines) and sigmoid
 7 ($|x_{\alpha\beta}|=4$: thick dashed lines) shape of density dependence in dispersal.

8
 9 Figure 2. Dynamics and spatial synchrony of the prey in predator-prey metacommunities as
 10 functions of its maximal dispersal rate (d_n). Top diagrams illustrate the various cases
 11 studied: N and P represent prey and predator densities; dispersal of each species is
 12 represented by a wide white arrow; positive or negative effects of densities on dispersal are
 13 represented by thin solid arrows with a + or a - sign. Figures in the first column (A and D)
 14 present results when dispersal is constant in both species. In the second column (B and E),
 15 we present results for (intra- and interspecific) density-dependent dispersal in the prey. In
 16 the third column (C and F), we present results for (intra- and interspecific) density-
 17 dependent dispersal in the predator. We present results for $d_n = 100 d_p$ ($d_n > d_p$) and for $d_p =$
 18 $100 d_n$ ($d_p > d_n$) in the first (A,B and C), and in the second (D, E and F) row, respectively.
 19 Markers on curves (except for A and D) indicate what type of density dependence the curve
 20 refers to: intraspecific (dots) or interspecific (triangles). The nature of dynamics obtained
 21 using the Lyapunov exponent is represented on curves: chaotic dynamics (with colour
 22 thickening) or periodic dynamics (without colour thickening). The specific colours used
 23 (gray, cyan and red) as well as the position of the thickening (above or under the curve) only
 24 help, in addition to curve markers, to distinguish between the different curves and do not
 25 have any further meaning. Notice on figures D, E, F ($d_p > d_n$) the two coexisting attractors
 26 (synchronous and asynchronous) for some dispersal rate values. Parameters values are the
 27 following. Constant dispersal: $x_{\alpha\beta}=0$; positive density-dependent dispersal: $x_{\alpha\beta}=4$
 28 ($\alpha\beta=nn,np,pp$); negative density-dependent dispersal: $x_{pn}=-4$. Other parameters: $S_{nn}=18$,
 29 $S_{np}=2$, $S_{pp}=2$, $S_{pn}=18$; local interactions: $r=10$, $K=25$, $b=11$, $c=1$, $m=10$.

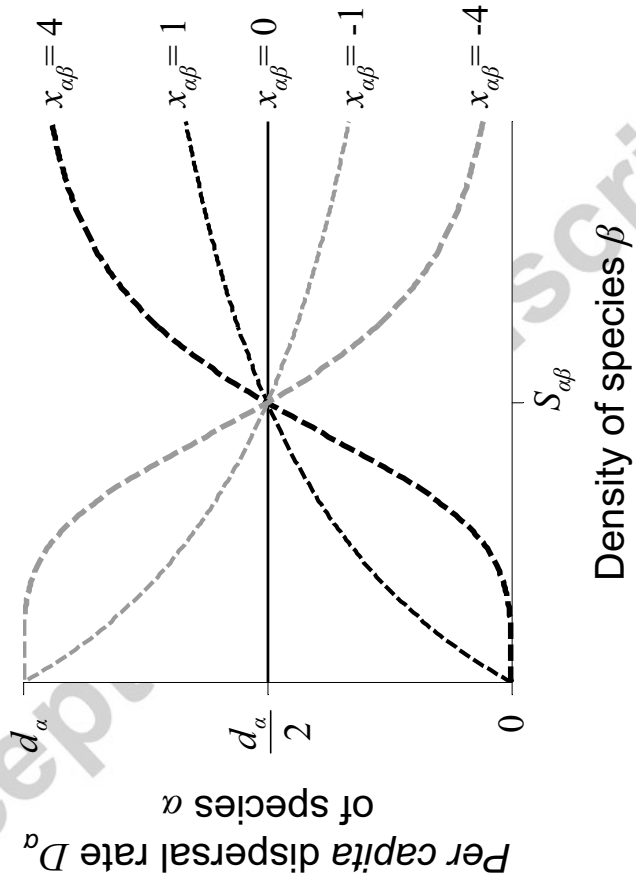
30
 31 Figure 3. Temporal mean of regional density (upper sub-graph) and coefficient of variation
 32 (CV, lower sub-graph) of the prey in predator-prey metacommunities as functions of its
 33 maximal dispersal rate (d_n). See legend of figure 2.

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

4

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

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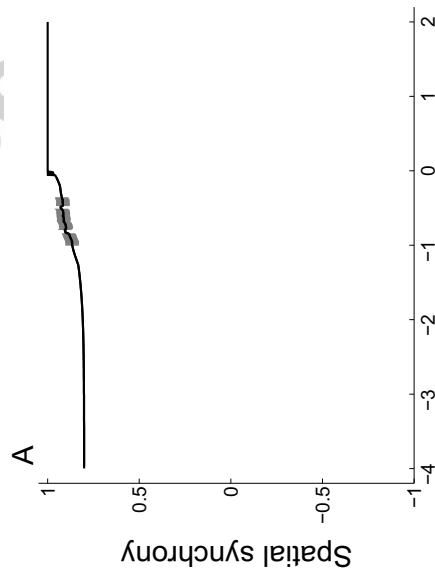


Constant dispersal
in the prey and the predator



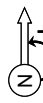
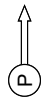
— periodic

▬ chaotic



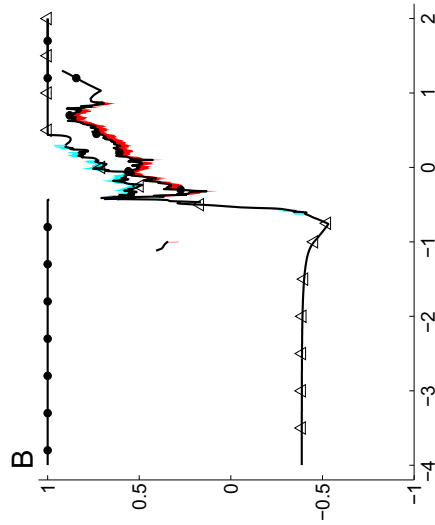
$$d_p > d_u$$

Density-dependent dispersal
in the prey

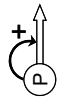


— periodic

▬ chaotic

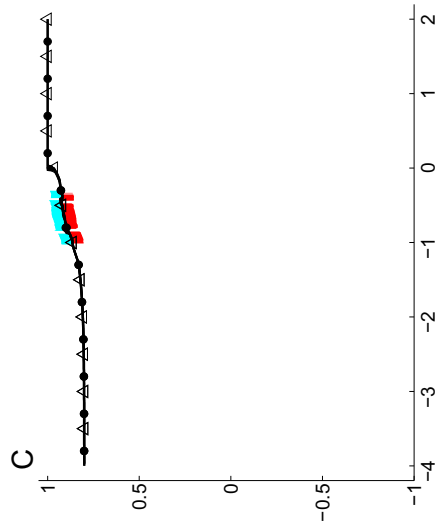


Density-dependent dispersal
in the predator

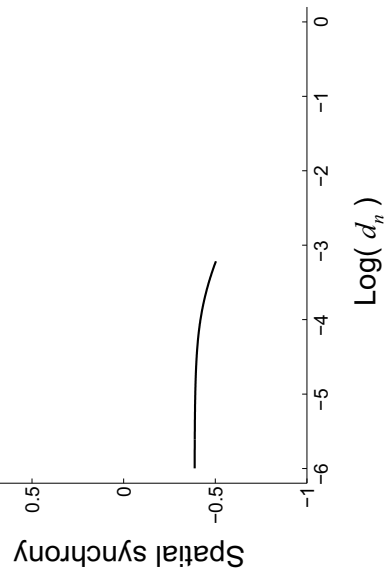


— periodic

▬ chaotic

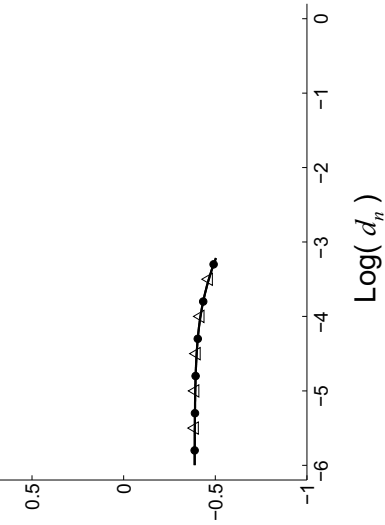


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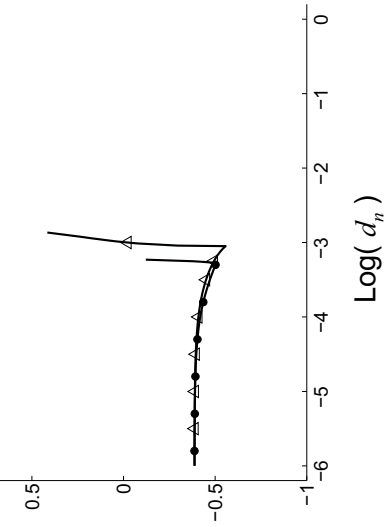


$$d_p > d_u$$

E



F



$\text{Log}(d_n)$

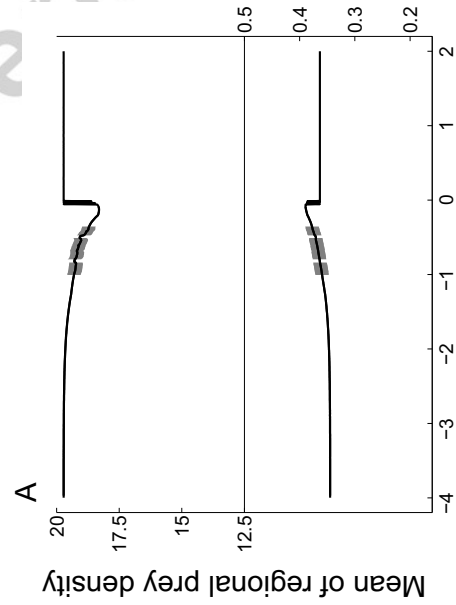
$\text{Log}(d_n)$

$\text{Log}(d_n)$

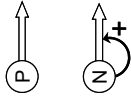
Constant dispersal
in the prey and the predator



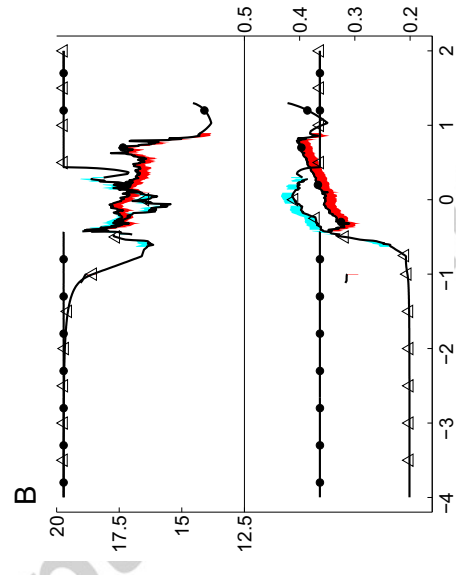
— periodic
■ chaotic



Density-dependent dispersal
in the prey



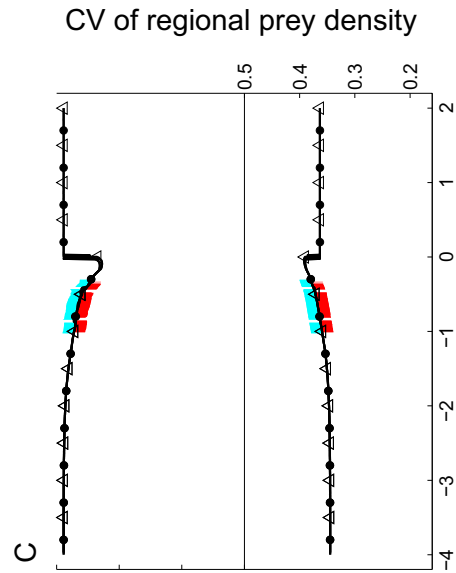
— periodic
■ chaotic



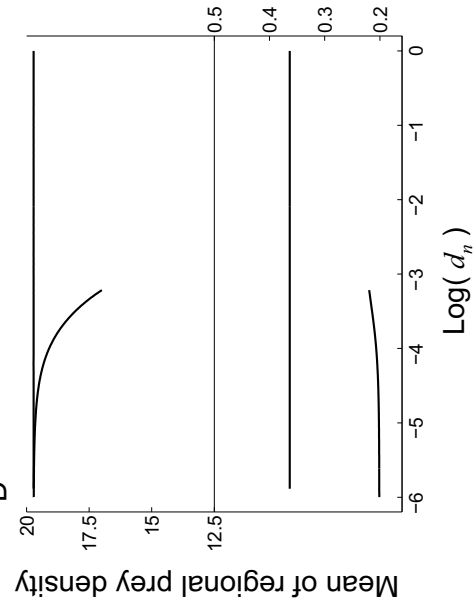
Density-dependent dispersal
in the predator



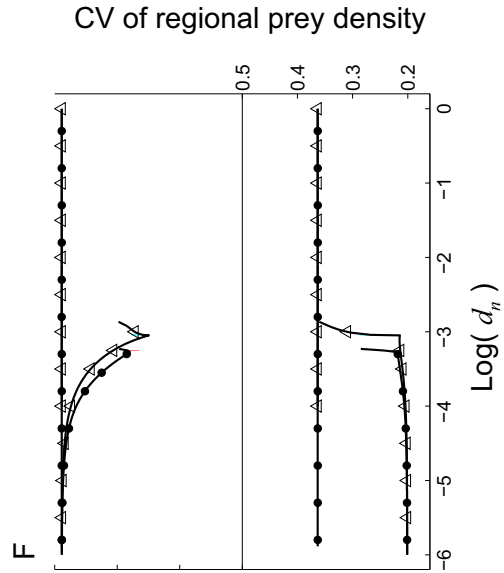
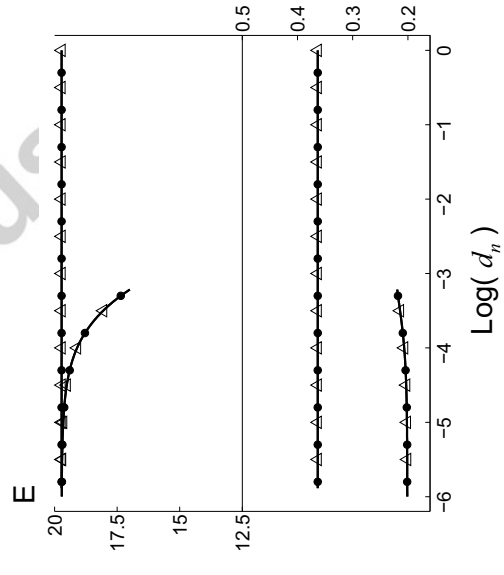
— periodic
■ chaotic



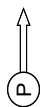
$$d^d > d^u$$



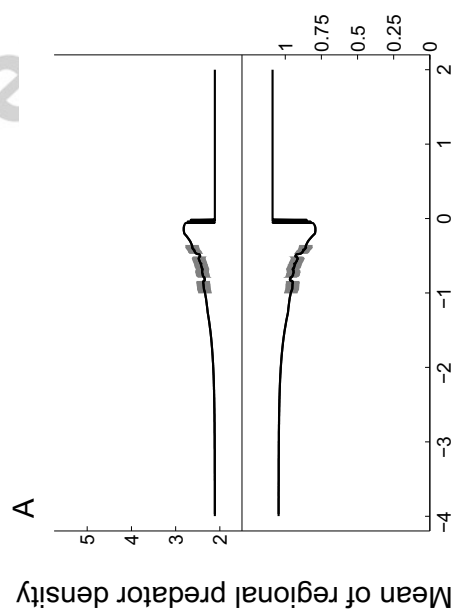
$$d^d > d^u$$



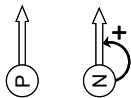
Constant dispersal
in the prey and the predator



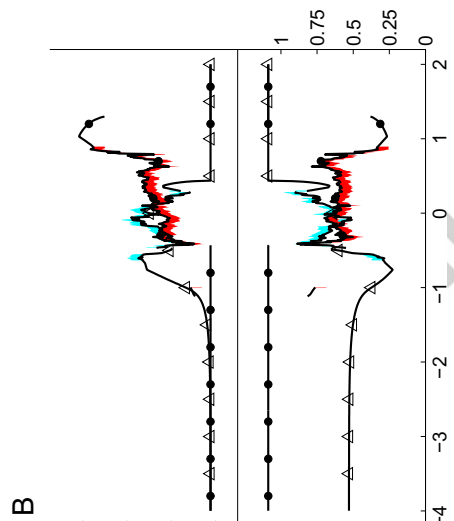
— periodic
▬ chaotic



Density-dependent dispersal
in the prey



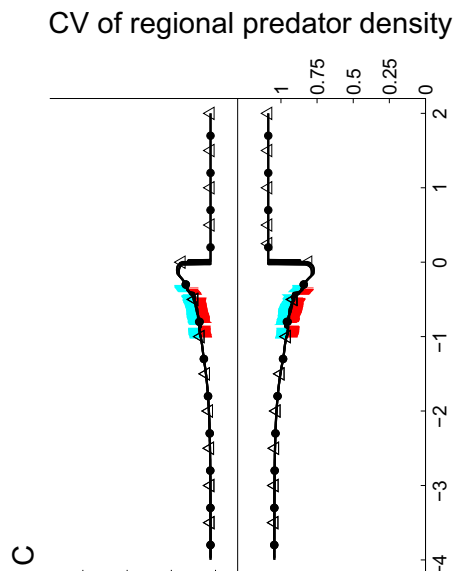
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▬ chaotic



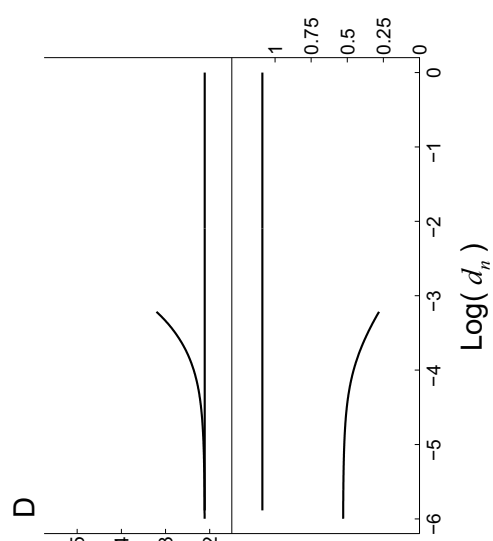
Density-dependent dispersal
in the predator



— periodic
▬ chaotic

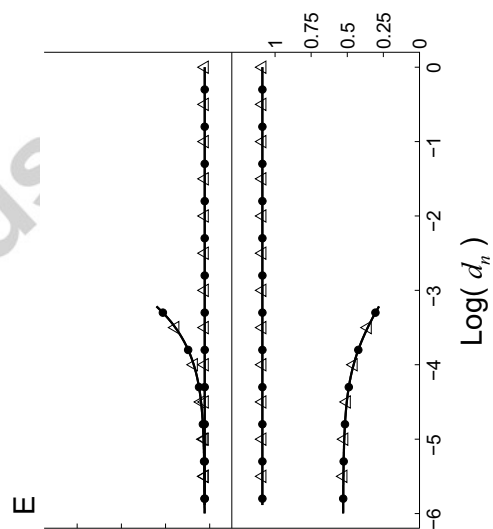


Mean of regional predator density

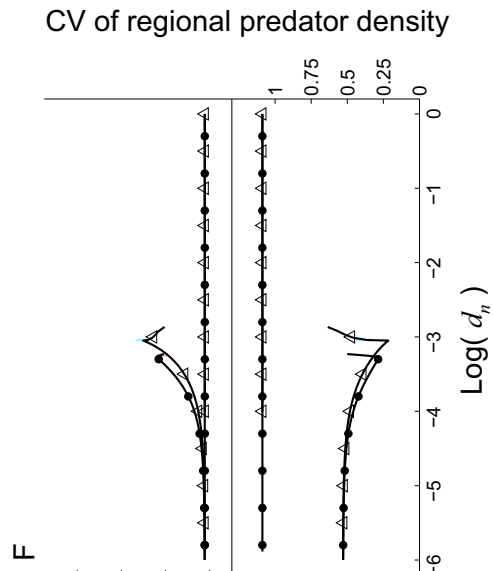


$$d^d < d^u$$

CV of regional predator density



CV of regional predator density



$$d^u > d^d$$

