

Two-patch population models with adaptive dispersal: the effects of varying dispersal speeds

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Abstract The population-dispersal dynamics for predator–prey interactions and two competing species in a two patch environment are studied. It is assumed that both species (i.e., either predators and their prey, or the two competing species) are mobile and their dispersal between patches is directed to the higher fitness patch. It is proved that such dispersal, irrespectively of its speed, cannot destabilize a locally stable predator–prey population equilibrium that corresponds to no movement at all. In the case of two competing species, dispersal can destabilize population equilibrium. Conditions are given when this cannot happen, including the case of identical patches.

Keywords Competition · Dispersal · Evolution · Habitat selection · Ideal free distribution · Predator · Prey · Population dynamics

Mathematics Subject Classification 34D20 · 92D25 · 92D40 · 92D50

1 Introduction

As [Levin \(1992\)](#) argued in his MacArthur award lecture, the problem of pattern and scale remains the central problem in ecology. For problems related to time scales, the crucial question is if and how do behavioral, ecological and evolutionary processes combine and influence each other. Do behavioral processes that proceed on time scales of minutes or hours attenuate on a longer population time scale of days, weeks, or

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years? Do processes on the population time scale influence evolutionary processes that run on the scale of hundreds and thousands of years? One reason why behavioral ecology has developed in separation from population ecology was the belief that processes operating on one time scale have little or no bearing on processes operating on a different time scale. However, recent models that combine different time scales challenge this view. In the case where animal behavior operates on a fast time scale, game theoretical approaches are used to determine optimal strategies at current population sizes. These optimal strategies are then fed back to population dynamics and the corresponding models predict that adaptive animal behaviors have the potential to promote species coexistence (for recent reviews see [Bolker et al. 2003](#); [Werner and Peacor 2003](#); [Abrams 2010](#)). Similarly, models that assume fast population dynamics and slow evolutionary processes show that traits change with changes in population densities. Trait dynamics in this case are described by the canonical equation of adaptive dynamics (e.g., [Geritz et al. 1998](#); [Abrams 2005](#); [Vincent and Brown 2005](#); [Dercole and Rinaldi 2008](#)). Both these approaches reduce complexity of the resulting model because the time scale separation reduces the number of differential equations that describe the system under study. The question that arises is then: Are predictions based on these models still valid when less extreme (or no) time scale separation is assumed? In this article we study this question in the context of population-dispersal models.

Models that consider population dynamics together with dispersal in a multi patch environment were thoroughly studied in the literature on evolution of dispersal (e.g., [Gadgil 1971](#); [Hamilton and May 1977](#); [Comins et al. 1980](#); [Hastings 1983](#); [Holt 1985](#); [McPeck and Holt 1992](#); [Holt and McPeck 1996](#); [Amarasekare 1998](#); [Diffendorfer 1998](#); [Dieckmann et al. 1999](#); [Ferriere et al. 2000](#); [Holt and Barfield 2001](#); [Donahue et al. 2003](#); [Padrón and Trevisan 2006](#); [Cantrell et al. 2007](#)) and on metapopulation dynamics ([Levin 1974](#); [Hassell et al. 1991](#); [Bascompte and Solé 1995](#); [Hassell et al. 1995](#); [Ruxton 1996](#); [Tilman and Kareiva 1997](#); [Hanski and Gilpin 1997](#); [Rohani and Ruxton 1999b](#); [Hanski 1999](#)). These models assume that individuals interact in patches between which they can also disperse. The dispersal rates between patches are assumed to be fixed, often corresponding to random dispersal. The main questions of these models are (1) what are the evolutionarily stable patterns of dispersal (i.e., what are the conditions that dispersal rates must satisfy so that individuals using a different dispersal strategy cannot invade residents) and (2) how dispersal influences species persistence.

One path to investigate these questions follows the classical idea of evolutionary ecology where the less fit phenotypes are replaced in evolution by fitter ones. In the context of evolution of dispersal, phenotypes are characterized by their dispersal properties. [Fretwell and Lucas \(1969\)](#) introduced the concept of the ideal free distribution (IFD) under which individuals in all occupied patches have the same fitness. [Cressman and Křivan \(2006\)](#) proved that the IFD is an evolutionarily stable strategy (ESS) of the habitat selection game (reviewed in [Křivan et al. 2008](#)). These game theoretical concepts do not deal with explicit dispersal mechanisms. Fixed dispersal rates that lead to the IFD when population dynamics are at an equilibrium are called balanced dispersal ([Holt 1985](#)). [Cantrell et al. \(2007\)](#) showed (in multiple species and/or multiple patches) that only those dispersal rates that lead to the IFD can be evolutionarily stable.

A second path of studies focuses on the stabilizing properties of dispersal on otherwise unstable population dynamics. It was shown that passive animal dispersal

at particular fixed rates can stabilize otherwise unstable predator–prey dynamics (e.g., [Holt 1984, 1985](#); [Murdoch et al. 2003](#)). This is because passive dispersal often causes sufficient negative density dependence in recruitment rates to stabilize population dynamics at an equilibrium. Thus, locally unstable population dynamics can lead to stability at the metapopulation level. However, for this to happen, heterogeneity in either patch population dynamics and/or dispersal rates are needed. In addition, dispersal rates cannot be so high that they synchronize local population dynamics across patches, but must be high enough to generate strong enough negative density dependence that can stabilize population dynamics.

Other models have been developed whereby the above fixed dispersal rates that characterize each phenotype are replaced by the assumption that individuals can quickly adjust their dispersal to reflect changes in patch occupancy ([Křivan and Sirot 2002](#); [Cressman et al. 2004](#); [Cressman and Křivan 2006](#)). In fact, these works often assume that dispersal strategy follows changes in population densities infinitely fast. Interestingly, it was shown (e.g., [Cressman et al. 2004](#)) that fast adaptive animal dispersal can destabilize the stable population equilibrium of two competing species that do not disperse at all. [Abrams et al. \(2007\)](#) analyzed this case in more detail. In particular, they relaxed the assumption of complete time scale separation between dispersal and population dynamics. Using numerical simulations, they showed that the predicted instability of the competition equilibrium due to fast dispersal led to fluctuations in population densities as there was no stable equilibrium point independent of the specific details of the dispersal dynamics. Furthermore, they also showed that different forms of these dispersal dynamics have a large effect on the population dynamics (see also [Abrams 2007, 2010](#)).

The idea that different processes operate on different time-scales was recently challenged in a number of articles on “rapid evolution” where evolutionary processes have a comparable time scale as population dynamics (for examples of such rapid evolution, see [Wikelski and Thom 2000](#); [Yalden 2000](#); [Relyea and Auld 2004](#); [Losos et al. 2006](#)). Changes in animal behaviors can take longer and run on a similar time scale as population dynamics. Thus, one has to accept that in some cases there is no clear time-scale separation of ecological processes. It is then important to understand what happens when behavior, population dynamics and evolution run on comparable time-scales. This is certainly true for models of dispersal. Dispersal can occur on a variety of time scales ranging from very fast to very slow, relative to population dynamics. So, it is important to better understand the effect of different time scales on population-dispersal dynamics.

In this article, we focus on models that combine population dynamics and adaptive dispersal in a two-patch environment. These models describe, in order, a single species, a predator–prey model, and a two competing species model in a two-patch environment. The dispersal between patches is assumed to be such that individuals tend to move to patches with the highest fitness. We will show that, under these assumptions, we can study analytically how population numbers and distributions depend on the scales on which demographic and distributional dynamics operate. In particular, we analyze how and if dispersal speed relative to demographic changes influences population stability and distribution.

2 Single species

We start with a single species in a two-patch environment. Population-dispersal dynamics are described by

$$\begin{aligned}\frac{dx_1}{dt} &= x_1 f_1(x_1) - \delta(d_{12}x_1 - d_{21}x_2), \\ \frac{dx_2}{dt} &= x_2 f_2(x_2) - \delta(d_{21}x_2 - d_{12}x_1),\end{aligned}\quad (1)$$

where x_i denotes population density in patch i ($i = 1, 2$), f_i is the patch specific per capita population growth rate, δ is the dispersal speed, and d_{ij} is the probability of dispersing from patch i to patch j . Thus, d_{ij} models animal preferences for the two habitats. The usual analysis of such models first calculates the equilibrium as a function of model parameters and then studies its local stability. When individuals do not disperse ($\delta = 0$), the populations in each patch evolve independently. Thus, for simple density dependent models such as logistic growth where f_i is a linear function, one solves the system of linear equations $f_i = 0$ ($i = 1, 2$) to find the non-trivial population equilibrium. However, the same model with dispersal ($\delta > 0$) is much more difficult to analyze, because we need to solve a system of two coupled quadratic equations to get the interior (i.e., where both x_1 and x_2 are positive) equilibrium. Although this is possible (computer algebra systems such as Mathematica handle it routinely), the resulting formulas are quite complicated. They can be used to study numerically the dependence of the equilibrium on a parameter. In this article, we are particularly interested in the effect of dispersal speed δ on the stability of the population equilibrium. When δ is small relative to demographic parameters, dispersal operates on a slow time scale when compared to population demography and vice versa. That is, manipulating δ allows us to effectively change time scales on which behavioral and population processes operate. Thus, we can ask, for example, whether slowly dispersing populations can influence relatively fast population dynamics, or vice versa.

To illustrate these ideas, Fig. 1a shows dependence of population equilibria in two patches as a function of dispersal speed when population dynamics are described by the logistic equation ($f_i = r_i(1 - x_i/K_i)$). When individuals do not disperse ($\delta = 0$), population densities reach patch carrying capacities ($K_1 = 10, K_2 = 1$ in Fig. 1a) and patch payoffs measured as the per capita population growth rate are the same (and equal 0, Fig. 1b). Thus, the corresponding equilibrium distribution $u_i = K_i/(K_1 + K_2)$ (Fig. 1c) is the ideal free distribution (i.e., IFD, [Fretwell and Lucas 1969](#)). As individuals start to disperse, one patch (dashed line) will become overpopulated, while the other patch (solid line) will be underpopulated, and, generically, the corresponding distribution will deviate from the IFD. Without any dispersal, it is obvious that the equilibrium is globally stable. However, one can wonder what happens when animals start to disperse. Provided population growth rate in each patch is negatively density dependent (not necessarily described by logistic growth), the interior population-distributional equilibrium will stay globally asymptotically stable regardless of dispersal speed ([Appendix A](#)). This clearly shows that, in the case of a single population in a two-patch environment population, stability is independent of the dispersal speed.

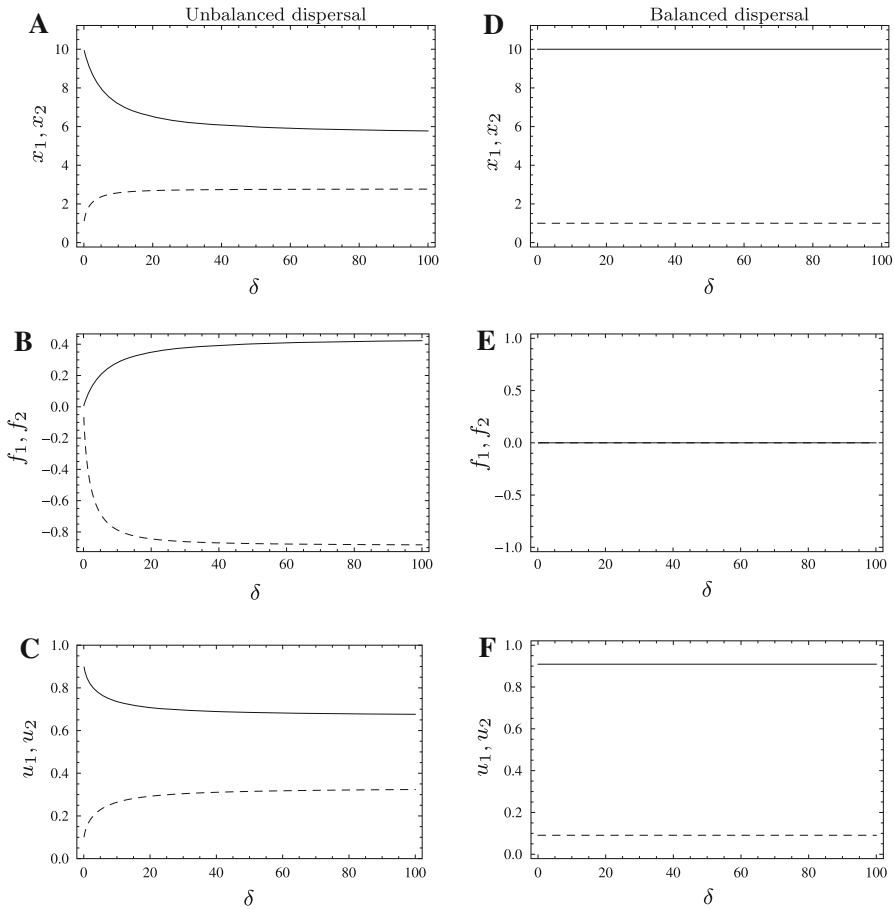


Fig. 1 This figure shows population-distribution dynamics for a two-patch logistic growth model as a function of dispersal speed δ . The *left panels* assume unbalanced dispersal rates ($d_{12} = 0.1$, $d_{21} = 0.2$), while the *right panels* assume balanced dispersal rates ($d_{12} = 0.1$, $d_{21} = 1$). The *top panels* show dependence of the equilibrium population densities, middle panels show fitness in patch 1 (*solid line*) and in patch 2 (*dashed line*), *bottom panels* show the corresponding distribution of the population in patch 1 (*solid line*) and in patch 2 (*dashed line*). Parameters: $r_1 = 1$, $r_2 = 0.5$, $K_1 = 10$, $K_2 = 1$

However, the above situation is not evolutionarily stable, because a population using dispersal speed δ can be invaded and replaced by a population using a slower dispersal speed unless dispersal rates satisfy

$$\frac{d_{12}}{d_{21}} = \frac{K_2}{K_1}. \tag{2}$$

The only evolutionary stable strategy (ESS) is not to disperse at all (i.e., $\delta = 0$) (Hastings 1983; Holt 1985). When dispersal rates satisfy (2), the system is said to exhibit balanced dispersal (McPeck and Holt 1992; Holt and Barfield 2001). In this case, there is no net movement between patches when population abundances in both

patches are equal to patch carrying capacities. Thus, this situation is exactly the same as if there was no dispersal. This is confirmed in the right panels of Fig. 1 which show that neither equilibrium population densities, nor distribution depend on the dispersal speed δ if there is balanced dispersal. These dispersal rates are evolutionarily stable, because no mutant using a different dispersal strategy can invade a resident system using balanced dispersal (McPeck and Holt 1992; Cressman and Křivan 2006).

Although we can calculate the ESS dispersal rates from (2), this does not provide a mechanistic description of the underlying distributional dynamics that leads to balanced dispersal. In this article, we will assume that the net movement between patches is always toward the patch with the higher per capita growth rate (also called the patch payoff). That is, $d_{ji}x_j - d_{ij}x_i > 0$ when $f_i > f_j$. In fact, we will assume that net movement is described by

$$\delta(d_{ji}x_j - d_{ij}x_i) = D(x_i, x_j)(f_i - f_j) \quad (3)$$

where D is a nonnegative function of x_1 and x_2 . For technical reasons (specifically, to ensure that population densities cannot become negative), assume that D is a continuous function satisfying $D(x_1, 0) = D(0, x_2) = 0$ for all $x_i \geq 0$, $i = 1, 2$. Model (1) becomes

$$\begin{aligned} \frac{dx_1}{dt} &= x_1 f_1(x_1) + D(x_1, x_2)(f_1 - f_2), \\ \frac{dx_2}{dt} &= x_2 f_2(x_2) + D(x_1, x_2)(f_2 - f_1). \end{aligned} \quad (4)$$

With such adaptive dispersal rates, the positive equilibrium of the above model is independent of the dispersal rate D and it is the same as in the case where individuals do not disperse at all (i.e., $f_i = 0$ for $i = 1, 2$). Appendix A shows that when patch payoff is negatively density dependent, the population-distribution equilibrium of the above model (i.e., the patch carrying capacities K_1 and K_2) is globally asymptotically stable independently of dispersal speed. At this equilibrium, net dispersal (3) is zero and so dispersal rates are balanced (i.e., they satisfy Eq. (2)).

One particular realization of such dispersal rates is

$$d_{ij} = \max\{f_j - f_i, 0\} \frac{x_j}{x_1 + x_2}, \quad (5)$$

which leads to

$$D(x_1, x_2) = \delta \frac{x_1 x_2}{x_1 + x_2} \quad (6)$$

in (3). These dispersal rates assume that individuals (i) are attracted to patches that have a higher fitness when compared with the current patch, and (ii) the attraction is proportional to the number of conspecifics in the new patch. Such “packing behavior” was observed in birds (e.g., Ahlering and Faaborg 2009; Folmer et al. 2010). Thus, there is a trade-off in these dispersal rates because a higher number of conspecifics in a patch attracts new immigrants, but it also decreases patch payoff. In other words, individuals will not disperse to patches that are not occupied even if patch payoff there

was high (which can be due to the perception barrier that does not allow individuals to perceive patch quality), but they also will not immigrate to patches with a high number of conspecifics. The population-dispersal dynamics (1) with dispersal (5) are then equivalent to the population-distributional dynamics

$$\begin{aligned}\frac{dx}{dt} &= x(u_1 f_1(u_1 x) + u_2 f_2(u_2 x)) \\ \frac{du_1}{dt} &= (1 + \delta)u_1(1 - u_1)(f_1(u_1 x) - f_2(u_2 x))\end{aligned}\quad (7)$$

where $x = x_1 + x_2$ is the overall population abundance and $u_i = x_i/x$ is the corresponding population distribution across patches. That is, from the first equation, overall abundance evolves according to the average per capita growth rate $u_1 f_1(u_1 x) + u_2 f_2(u_2 x)$. Furthermore, the proportion of the population in the patch with the higher fitness increases by the second equation, which is known as the replicator equation (e.g., Taylor and Jonker 1978; Hofbauer and Sigmund 1998; Cressman and Křivan 2006) up to the factor $1 + \delta$. This form clearly shows how demographic and distributional time scales are related. If $\delta > 1$ ($\delta < 1$) then distributional dynamics operate on a faster (slower) time scale when compared to demographic processes.

Thus, with adaptive dispersal toward the patch with higher fitness, the stationary distribution is $u_i = K_i/(K_1 + K_2)$ and the overall equilibrium population abundance is $x = K_1 + K_2$ independently of the dispersal speed. Furthermore, changes in time scales do not influence stability of this population-dispersal equilibrium.

Similar results are known for models that assume non-adaptive dispersal. In particular, when the patches are identical (i.e., $f_1(x_1) = f_2(x_2)$ if $x_1 = x_2$), then the equilibrium for system (1) is the carrying capacity $K_1 = K_2$ in each patch for all choices of fixed δ and non-directional dispersal (i.e., dispersal is random and so $d_{12} = d_{21}$). Moreover, from the analysis at the beginning of this section, this population-dispersal equilibrium is asymptotically stable for all such dispersal rates. On the other hand, when there are two (or more) behavioral types in each patch, then time scales can influence stability if the random dispersal rates of the types are sufficiently different. This follows from Cressman and Vickers (1997) who show that Turing instabilities (Turing 1952) arise in corresponding single-species spatially-homogeneous models with continuous space. It also follows from the analysis of Jansen and Lloyd (2000) (see also Rohani and Ruxton 1999a; Cosner 2008) when the two behavioral types correspond to separate species such as predators and prey.

In the following two sections, we study whether time scales influence stability in multi-species environments where dispersal rates between the two patches and the speed of demographic changes can be species dependent (and where each species has only one behavioral type). We are particularly interested in this question when dispersal is adaptive and patches are not identical.

3 Predator–prey models with dispersal

We assume that predator fitness g_i ($i = 1, 2$) in each patch is an increasing function that depends only on prey density there (e.g., the standard Gause (Gause 1934)

predator–prey model satisfies this). With adaptive dispersal, the population–dispersal dynamics become

$$\begin{aligned} \frac{dx_1}{dt} &= x_1 f_1(x_1, y_1) + D_x(x, y)(f_1(x_1, y_1) - f_2(x_2, y_2)) \\ \frac{dx_2}{dt} &= x_2 f_2(x_2, y_2) + D_x(x, y)(f_2(x_2, y_2) - f_1(x_1, y_1)) \\ \frac{dy_1}{dt} &= y_1 g_1(x_1) + D_y(x, y)(g_1(x_1) - g_2(x_2)) \\ \frac{dy_2}{dt} &= y_2 g_2(x_2) + D_y(x, y)(g_2(x_2) - g_1(x_1)) \end{aligned} \tag{8}$$

where x_i and y_i are population abundances of prey and predators, respectively, in patch i ($= 1, 2$). In these equations, the dispersal rates $D_x(x, y)$ and $D_y(x, y)$ for prey and predator populations, respectively, are assumed to satisfy conditions as in (3) and (4) needed to keep the positive cone invariant.

In all our simulations with adaptive dispersal, the prey dispersal rate is taken explicitly as $D_x(x, y) = \delta_x \frac{x_1 x_2}{x_1 + x_2}$ (cf., Eq. (6)) and, similarly, for the predator dispersal rate, $D_y(x, y) = \delta_y \frac{y_1 y_2}{y_1 + y_2}$. Parameters δ_x and δ_y then continue to describe the prey and predator, respectively, dispersal speed. Changing these parameters allows us effectively to change dispersal versus population dynamics time scales. The above population dynamical model can then be equivalently rewritten using the overall prey and predator abundances and their distribution between patches

$$\begin{aligned} \frac{dx}{dt} &= x(u_1 f_1 + u_2 f_2) \\ \frac{dy}{dt} &= y(v_1 g_1 + v_2 g_2) \\ \frac{du_1}{dt} &= (1 + \delta_x)u_1(1 - u_1)(f_1 - f_2) \\ \frac{dv_1}{dt} &= (1 + \delta_y)v_1(1 - v_1)(g_1 - g_2) \end{aligned} \tag{9}$$

where u_i (v_i) is the fraction of prey (predators) in patch i ($i = 1, 2$), and x (y) is the overall prey (predator) population abundance.

In what follows, we will assume that there exists an interior equilibrium $(x_1^*, x_2^*, y_1^*, y_2^*)$ of the predator–prey population dynamics without any dispersal. We observe that this interior equilibrium is also an equilibrium of the model when populations do disperse (i.e., the equilibrium is independent of the dispersal rates). The following proposition is proved in Appendix B by linearizing (8) about the equilibrium. Global stability of the equilibrium remains an open problem.

Proposition 1 *Assume that $(x_1^*, x_2^*, y_1^*, y_2^*)$ is an interior equilibrium (i.e., both species coexist in both patches) of model (8) when $D_x = D_y = 0$. If*

$$\frac{\partial f_i}{\partial x_i}(x^*, y^*) < 0, \quad \frac{\partial f_i}{\partial y_i}(x^*, y^*) < 0, \quad \frac{dg_i}{dx_i}(x_i^*) > 0, \tag{10}$$

this equilibrium is locally asymptotically stable for the model with any choice of dispersal rates $D_x(x, y)$ and $D_y(x, y)$.

We remark that when there is no dispersal (i.e., $D_x = D_y = 0$), the inequalities (10) in the proposition are the standard assumptions (e.g., Allen 2007) that ensure the equilibrium is locally asymptotically stable in each patch i . In particular, since prey fitness decreases when either prey or predator density increases, and predator fitness increases with more prey, the trace of the Jacobian matrix is negative and the determinant is positive (see Appendix B). Proposition 1 states that dispersal cannot destabilize populations at this equilibrium. In other words, a stable predator–prey equilibrium without dispersal cannot be destabilized when individuals move adaptively between two patches. In particular, no instability driven by different predator and prey dispersal speeds can occur in these two-patch predator–prey models.

The result reported in Proposition 1 is similar to those in other studies of dispersal-driven instability when the patches are identical. In this case, a stable interior equilibrium (x_1^*, y_1^*) in patch one without dispersal corresponds to a spatially-homogeneous (i.e., $x_1^* = x_2^*$ and $y_1^* = y_2^*$) interior equilibrium of the population-dispersal dynamics under random dispersal. If fitness functions satisfy (10), it is well-known (Jansen and Lloyd 2000) that no instability produced by different predator and prey random dispersal rates can occur (i.e., no Turing instabilities (Turing 1952) can emerge in these models). In fact, even when dispersal is partially adaptive in the sense that prey increase their dispersal rate from a patch as the density of predators increase in this patch due to higher predation risk (or analogously, predators decrease their dispersal rate as prey density rises), Huang and Diekmann (2003) show Turing instabilities are impossible. Turing instabilities due to different dispersal rates for hosts and parasites (Briggs and Hoopes 2004) require that parasite growth rates also depend on parasite density (i.e., g_i is a function of both x_i and y_i).

3.1 Lotka–Volterra

The Lotka–Volterra predator–prey population-dispersal model in a two patch environment is

$$\begin{aligned}
 \frac{dx_1}{dt} &= x_1 \left(a_1 \left(1 - \frac{x_1}{K_1} \right) - \lambda_1 y_1 \right) + D_x(x, y) \\
 &\quad \times \left(a_1 \left(1 - \frac{x_1}{K_1} \right) - \lambda_1 y_1 - a_2 \left(1 - \frac{x_2}{K_2} \right) + \lambda_2 y_2 \right) \\
 \frac{dx_2}{dt} &= x_2 \left(a_2 \left(1 - \frac{x_2}{K_2} \right) - \lambda_2 y_2 \right) + D_x(x, y) \\
 &\quad \times \left(a_2 \left(1 - \frac{x_2}{K_2} \right) - \lambda_2 y_2 - a_1 \left(1 - \frac{x_1}{K_1} \right) + \lambda_1 y_1 \right) \\
 \frac{dy_1}{dt} &= y_1 (e_1 \lambda_1 x_1 - m_1) + D_y(x, y) (e_1 \lambda_1 x_1 - m_1 - e_2 \lambda_2 x_2 + m_2) \\
 \frac{dy_2}{dt} &= y_2 (e_2 \lambda_2 x_2 - m_2) + D_y(x, y) (e_2 \lambda_2 x_2 - m_2 - e_1 \lambda_1 x_1 + m_1).
 \end{aligned}
 \tag{11}$$

This is a special case of (8) where the fitness functions are given by $f_i(x_i, y_i) = a_i \left(1 - \frac{x_i}{K_i} \right) - \lambda_i y_i$ and $g_i(x_i) = e_i \lambda_i x_i - m_i$. The interior equilibrium $(x_1^*, x_2^*, y_1^*, y_2^*)$

of (11) exists (i.e., an equilibrium where both species are distributed over both patches) when there is no dispersal if and only if the equilibrium prey density x_i^* in each patch is less than its carrying capacity in the absence of predators (i.e., if and only if $x_i^* < K_i$). Specifically, the equilibrium is

$$(x_1^*, x_2^*, y_1^*, y_2^*) = \left(\frac{m_1}{e_1 \lambda_1}, \frac{m_2}{e_2 \lambda_2}, \frac{a_1(e_1 \lambda_1 K_1 - m_1)}{e_1 \lambda_1^2 K_1}, \frac{a_2(e_2 \lambda_2 K_2 - m_2)}{e_2 \lambda_2^2 K_2} \right). \quad (12)$$

The corresponding prey distribution is

$$u_1^* = \frac{e_2 m_1 \lambda_2}{e_1 m_2 \lambda_1 + e_2 m_1 \lambda_2}$$

while predator distribution is

$$v_1^* = \frac{a_1 e_2 K_2 \lambda_2^2 (m_1 - e_1 K_1 \lambda_1)}{a_1 e_2 K_2 \lambda_2^2 (m_1 - e_1 K_1 \lambda_1) + a_2 e_1 K_1 \lambda_1^2 (m_2 - e_2 K_2 \lambda_2)}.$$

For the Lotka–Volterra model (11) without dispersal (i.e., when $D_x = D_y = 0$), the interior equilibrium is globally asymptotically stable if it exists (Svirezhev and Logofet 1983; Křivan 2008). In particular, the fitness functions satisfy condition (10) and so, by Proposition 1, the interior equilibrium is also locally asymptotically stable for any dispersal speeds.

3.2 Rosenzweig–MacArthur model

Let h_i be the (positive) handling time of a captured prey in patch i in the standard Rosenzweig–MacArthur predator–prey model (e.g., Rosenzweig and MacArthur 1963; Hofbauer and Sigmund 1988; Křivan 2008) with the Holling type II functional response. Then, the fitness function for prey becomes

$$f_i = a_i \left(1 - \frac{x_i}{K_i} \right) - \frac{\lambda_i y_i}{1 + \lambda_i h_i x_i}, \quad i = 1, 2$$

and for predators

$$g_i = \frac{e_i \lambda_i x_i}{1 + \lambda_i h_i x_i} - m_i, \quad i = 1, 2.$$

The predator–prey model (8) then has the interior equilibrium

$$x_i^* = \frac{m_i}{(e_i - h_i m_i) \lambda_i}, \quad i = 1, 2$$

$$y_i^* = \frac{a_i e_i (e_i K_i \lambda_i - m_i (1 + h_i K_i \lambda_i))}{K_i (e_i - h_i m_i)^2 \lambda_i^2}, \quad i = 1, 2$$

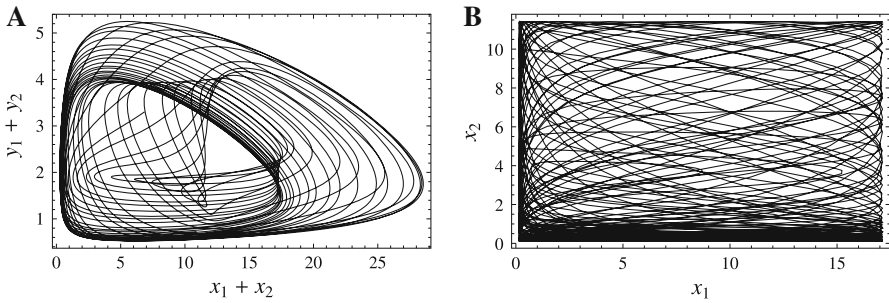


Fig. 2 Trajectories of the Rosenzweig–MacArthur model (13) with no dispersal fill the surface of a torus (Panel A). In panel B a trajectory is shown in (x_1, x_2) space. This leads to a Lissajous like curve. Parameters: $\delta_x = \delta_y = 0, a_1 = 1.5, a_2 = 0.5, e_1 = 0.15, e_2 = 0.1, m_1 = 0.4, m_2 = 0.2, K_1 = 25, K_2 = 20, \lambda_1 = 1, \lambda_2 = 1, h_1 = 0.1, h_2 = 0.1$

provided $h_i < e_i/m_i$ and $m_i < e_i \lambda_i K_i / (1 + h_i \lambda_i K_i)$. This latter inequality holds if and only if the equilibrium prey density is less than its carrying capacity in the absence of predators (i.e., if and only if $x_i^* < K_i$).

It is well-known (e.g., Hofbauer and Sigmund 1988; Křivan 2008) that, without dispersal, this interior equilibrium is globally asymptotically stable in patch i if and only if x_i^* is sufficiently large. For our model, global asymptotic stability occurs if and only if $x_i^* > \frac{h_i \lambda_i K_i - 1}{2 h_i \lambda_i}$ (if and only if $K_i < \frac{e_i + m_i h_i}{h_i \lambda_i (e_i - m_i h_i)}$). These are the conditions equivalent to the inequalities in (10). From Proposition 1, we again find that a stable predator–prey equilibrium without dispersal cannot be destabilized when individuals move adaptively between two patches. It is also well-known that, without dispersal, populations will fluctuate periodically as they approach a globally stable limit cycle in each patch when the predator–prey equilibrium is unstable in both patches. Generically, this limiting behavior results in aperiodic movement that fills the surface of a torus in the four-dimensional space (x_1, x_2, y_1, y_2) as shown in Fig. 2a. Projections to a plane (Fig. 2b shows projection to (x_1, x_2) plane) produces Lissajous curves (Greenslade 1993).

It is then interesting to study whether adaptive dispersal can stabilize unstable predator–prey equilibria when prey carrying capacities are large enough to produce stable population oscillations (i.e., $K_i > \frac{e_i + m_i h_i}{h_i \lambda_i (e_i - m_i h_i)}$ for at least one patch). This becomes especially interesting when comparing stability results under our adaptive dispersal to the known result that passive dispersal between patches can lead to negative density dependent recruitment rates provided fluctuations in population densities are asynchronous (Murdoch et al. 2003; Briggs and Hoopes 2004). This mechanism underlies deterministic metapopulation dynamics where populations can coexist on the global spatial scale despite local extinctions (Hanski 1999). The necessary conditions for such global stability are differences in patch or dispersal dynamics, and dispersal rates that are neither too high to synchronize local patch dynamics, nor too low to decouple patch dynamics.

To illustrate the above discussion, recall that our population dynamics in (8) assume prey have negative density dependent growth rates. If we replace the dispersal term in (8) by passive dispersal, i.e.,

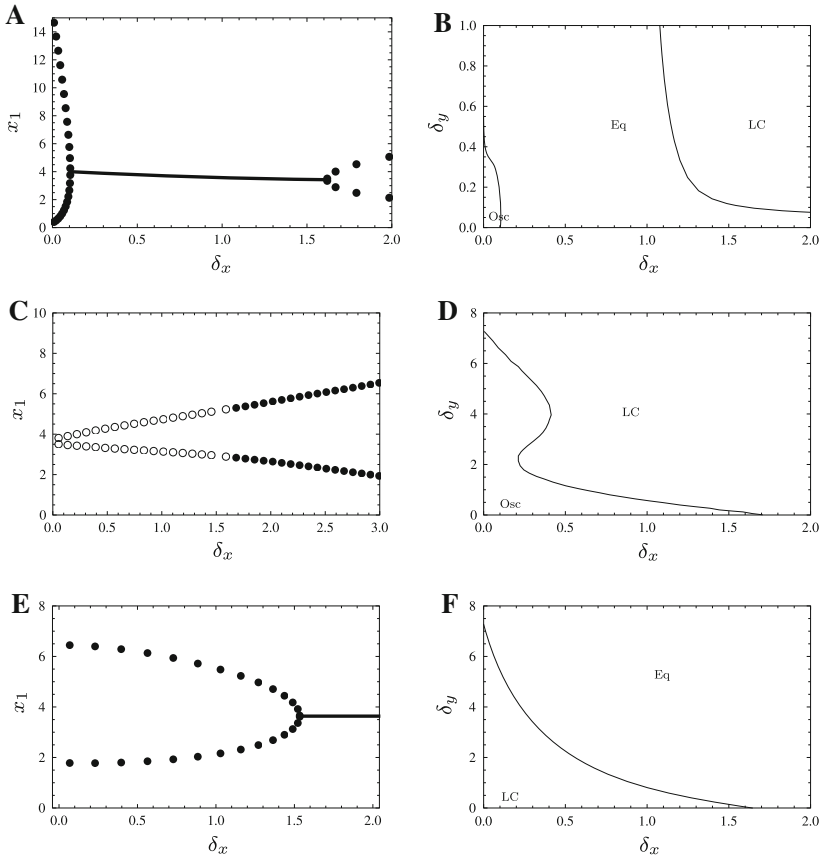


Fig. 3 This figure describes qualitative properties of trajectories for the Rosenzweig–MacArthur predator–prey model. The *top two panels* show simulations of model (13) with random dispersal between patches ($d_{12} = d_{21} = 1$ and $\eta_{12} = \eta_{21} = 1$) when predators and prey coexist along a limit cycle in each patch without any dispersal ($K_1 = 25, K_2 = 20$). These simulations document that intermediate values of random dispersal stabilize population dynamics at an equilibrium. *Solid dots* in the *left panels* that have predator dispersal rate fixed at 0.1 correspond to maxima and minima of locally stable periodic trajectories and lines describe locally stable equilibria. The *right top panel* shows the two curves where a Hopf bifurcation occurs at which the locally stable equilibrium loses its stability and a locally stable limit cycle (denoted as LC) appears. In the *lower left corner* (denoted as *Osc*), this limit cycle for yet smaller dispersal rates (not shown here) loses its stability and trajectories fill the surface of a torus. The *middle and bottom panels* correspond to model (8) with adaptive dispersal. In the *middle two panels*, without any dispersal, population dynamics oscillate in both patches ($K_1 = 18, K_2 = 17$). These numerical simulations document that adaptive dispersal cannot stabilize population dynamics at an equilibrium. The *left panel* shows how the locally stable limit cycle (*solid dots*) becomes unstable (*empty dots*) at low prey dispersal rates (predator dispersal rate δ_y is fixed at 0.1), while the *right panel* shows the curve of Neimark–Sacker bifurcations along which the locally stable limit cycle bifurcates to an aperiodic motion on a torus. In the *bottom panels*, without any dispersal, population dynamics oscillate only in patch 1 and settle to an equilibrium in patch 2 ($K_1 = 18, K_2 = 10$). These numerical simulations show that adaptive dispersal with sufficiently high prey and/or predator dispersal rates can stabilize population dynamics at an equilibrium. The *left panel* shows qualitative behavior of the model as a function of prey dispersal only (δ_y is fixed at 0.1), while the *right panel* shows regions of prey and predator dispersal rates where either populations coexist at an equilibrium, or along a limit cycle. These two parameter regions are separated by the Hopf bifurcation curve. Parameters: $a_1 = 1.5, a_2 = 0.5, e_1 = 0.15, e_2 = 0.1, m_1 = 0.4, m_2 = 0.2, \lambda_1 = 1, \lambda_2 = 1, h_1 = 0.1, h_2 = 0.1$

$$\begin{aligned}
 \frac{dx_1}{dt} &= x_1 f_1(x_1, y_1) - \delta_x(d_{12}x_1 - d_{21}x_2) \\
 \frac{dx_2}{dt} &= x_2 f_2(x_2, y_2) - \delta_x(d_{21}x_2 - d_{12}x_1) \\
 \frac{dy_1}{dt} &= y_1 g_1(x_1) - \delta_y(\eta_{12}y_1 - \eta_{21}y_2) \\
 \frac{dy_2}{dt} &= y_2 g_2(x_2) - \delta_y(\eta_{21}y_2 - \eta_{12}y_1)
 \end{aligned}
 \tag{13}$$

then the recruitment rate would possibly add another negative density dependence. A combination of these two effects can therefore increase stability of the predator–prey system (13) as documented in the top panels of Fig. 3 where intermediate values of passive prey and/or predator dispersal stabilizes otherwise unstable population dynamics at an equilibrium. Figure 3b shows two Hopf bifurcation curves across which the locally stable equilibrium becomes destabilized and a limit cycle occurs. We remark that for very low dispersal rates (not depicted in Fig. 3a) the limit cycle becomes unstable and trajectories will fill the surface of a torus (as shown in Fig. 2).

Appendix B shows that our model (8) (which assumes adaptive dispersal) leads to strikingly different predictions. In fact, adaptive dispersal cannot stabilize population dynamics if oscillations occur in both patches (Fig. 3, middle panels). The left panel shows that a locally stable limit cycle (solid dots) loses its stability when prey dispersal rate is too small (empty dots). The right panel shows the Neimark–Sacker bifurcation curve (Kuznetsov 1995). When traversing this curve from the right, the locally stable limit cycle loses its stability and trajectories fill the surface of a torus (c.f. Fig. 2). Only if population dynamics settle at an equilibrium in one patch and oscillate in the other patch, can high enough dispersal rates stabilize population dynamics at an equilibrium (Appendix B and bottom panels of Fig. 3).

4 Competing species with dispersal

Here we consider two competing species in a two-patch environment. Population-dispersal dynamics in a two-patch environment are described as

$$\begin{aligned}
 \frac{dx_1}{dt} &= x_1 f_1(x_1, y_1) + D_x(x, y)(f_1(x_1, y_1) - f_2(x_2, y_2)) \\
 \frac{dx_2}{dt} &= x_2 f_2(x_2, y_2) + D_x(x, y)(f_2(x_2, y_2) - f_1(x_1, y_1)) \\
 \frac{dy_1}{dt} &= y_1 g_1(x_1, y_1) + D_y(x, y)(g_1(x_1, y_1) - g_2(x_2, y_2)) \\
 \frac{dy_2}{dt} &= y_2 g_2(x_2, y_2) + D_y(x, y)(g_2(x_2, y_2) - g_1(x_1, y_1))
 \end{aligned}
 \tag{14}$$

where x_i and y_i are population abundances of the two competing species in patch i ($= 1, 2$). We assume that $\frac{\partial f_i}{\partial x_i} < 0$, $\frac{\partial f_i}{\partial y_i} < 0$, $\frac{\partial g_i}{\partial x_i} < 0$, $\frac{\partial g_i}{\partial y_i} < 0$ so that model (14) describes competition between the two species. In addition, assume that, without any dispersal, the two species coexist at a stable equilibrium in each patch. In particular, this requires

$$\frac{\partial f_i}{\partial y_i} \frac{\partial g_i}{\partial x_i} < \frac{\partial f_i}{\partial x_i} \frac{\partial g_i}{\partial y_i}, \quad i = 1, 2,$$

i.e., the interspecific competition is weaker than intraspecific competition. This equilibrium is also an equilibrium for the system with adaptive dispersal and our interest is to study its stability as a function of dispersal rates D_x and D_y . The following Proposition is proved in Appendix C.

Proposition 2 *Let us assume that model (14) with $D_x = D_y = 0$ has an interior equilibrium at which both species coexist at both patches. Let $A = \frac{\partial f_1}{\partial y_1} \frac{\partial g_1}{\partial x_1} - \frac{\partial f_1}{\partial x_1} \frac{\partial g_1}{\partial y_1}$, $B = \frac{\partial f_2}{\partial y_2} \frac{\partial g_2}{\partial x_2} - \frac{\partial f_2}{\partial x_2} \frac{\partial g_2}{\partial y_2}$, $C = \frac{\partial f_1}{\partial x_1} \frac{\partial g_2}{\partial y_2} - \frac{\partial f_1}{\partial y_1} \frac{\partial g_2}{\partial x_2}$, $D = \frac{\partial f_2}{\partial x_2} \frac{\partial g_1}{\partial y_1} - \frac{\partial f_2}{\partial y_2} \frac{\partial g_1}{\partial x_1}$ be evaluated at this equilibrium. From the above discussion, if $A < 0$ and $B < 0$, then the equilibrium is locally asymptotically stable without dispersal.*

Assume that A, B are both negative. If the equilibrium remains locally asymptotically stable independent of the dispersal rates D_x and D_y , then $C + D > A + B$. Conversely, if $C + D > 0$, then the equilibrium is locally asymptotically stable for any dispersal rates D_x and D_y .

Although the two species do compete only if they are in the same patch, the above proposition tells us that when these species disperse, it is not enough to consider competition within patches only. In fact, to ensure stability of the interior equilibrium, we must look at the virtual competition between species x in patch 1 and species y in patch 2 and between species x in patch 2 and species y in patch 1, as if they were competing (i.e., at the expressions C and D in Proposition 2). From Appendix C, it is clear that adding sufficiently high dispersal introduces instability when $A + B > C + D$ (see also Fig. 3).

On the other hand, by the final statement of Proposition 2, adaptive dispersal cannot destabilize an otherwise stable equilibrium when space is homogeneous (and so competition is patch independent). In this case, each species has the same fitness function in both patches (i.e., $f_1 = f_2, g_1 = g_2$) and so $C = -A > 0$ and $D = -B > 0$. Thus the interior equilibrium is locally asymptotically stable for all dispersal rates if and only if it is locally asymptotically stable when there is no dispersal. That is, pattern formation similar to a Turing instability cannot occur in the two-patch competition model with adaptive dispersal.

In the case of the Lotka–Volterra competition model, species one fitness in patch i ($i = 1, 2$) is

$$f_i = a_i \left(1 - \frac{x_i}{K_i} - \alpha_i \frac{y_i}{K_i} \right),$$

and species two fitness is

$$g_i = b_i \left(1 - \frac{y_i}{L_i} - \beta_i \frac{x_i}{L_i} \right),$$

and population dynamics are

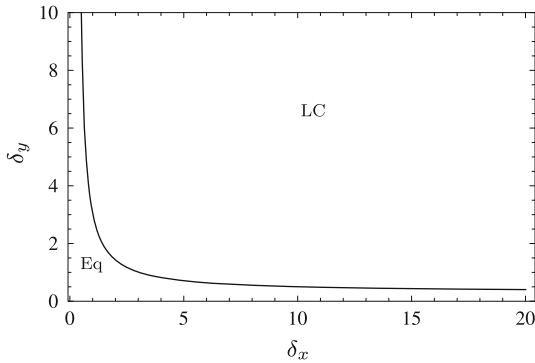


Fig. 4 This figure documents the case where strong enough dispersal destabilizes competition dynamics (15) when interspecific competition is patch dependent. The curve corresponds to the Hopf bifurcation curve in the $\delta_x - \delta_y$ parameter plane for the competition model (15). The curve shown is the set of dispersal rates at which the interior equilibrium is destabilized by the Hopf bifurcation. For dispersal rates to the left and below this curve, population dynamics converge to an equilibrium, while to the right and above, the interior equilibrium is unstable and a locally stable limit cycle exists. Parameters: $a_1 = 1, a_2 = 0.1, b_1 = 0.1, b_2 = 1, L_1 = 2, L_2 = 19, K_1 = 19, K_2 = 2, \alpha_1 = 9, \alpha_2 = 0.1, \beta_1 = 0.1, \beta_2 = 9$.

$$\begin{aligned}
 \frac{dx_1}{dt} &= x_1 a_1 \left(1 - \frac{x_1}{K_1} - \alpha_1 \frac{y_1}{K_1} \right) \\
 &\quad + D_x(x, y) \left(a_1 \left(1 - \frac{x_1}{K_1} - \alpha_1 \frac{y_1}{K_1} \right) - a_2 \left(1 - \frac{x_2}{K_2} - \alpha_2 \frac{y_2}{K_2} \right) \right) \\
 \frac{dx_2}{dt} &= x_2 a_2 \left(1 - \frac{x_2}{K_2} - \alpha_2 \frac{y_2}{K_2} \right) \\
 &\quad + D_x(x, y) \left(a_2 \left(1 - \frac{x_2}{K_2} - \alpha_2 \frac{y_2}{K_2} \right) - a_1 \left(1 - \frac{x_1}{K_1} - \alpha_1 \frac{y_1}{K_1} \right) \right) \\
 \frac{dy_1}{dt} &= y_1 b_1 \left(1 - \frac{y_1}{L_1} - \beta_1 \frac{x_1}{L_1} \right) \\
 &\quad + D_y(x, y) \left(b_1 \left(1 - \frac{y_1}{L_1} - \beta_1 \frac{x_1}{L_1} \right) - b_2 \left(1 - \frac{y_2}{L_2} - \beta_2 \frac{x_2}{L_2} \right) \right) \\
 \frac{dy_2}{dt} &= y_2 b_2 \left(1 - \frac{y_2}{L_2} - \beta_2 \frac{x_2}{L_2} \right) \\
 &\quad + D_y(x, y) \left(b_2 \left(1 - \frac{y_2}{L_2} - \beta_2 \frac{x_2}{L_2} \right) - b_1 \left(1 - \frac{y_1}{L_1} - \beta_1 \frac{x_1}{L_1} \right) \right).
 \end{aligned} \tag{15}$$

The interior equilibrium where both species are distributed over both patches is

$$x_i^* = \frac{K_i - \alpha_i L_i}{1 - \alpha_i \beta_i}, \quad y_i^* = \frac{L_i - \beta_i K_i}{1 - \alpha_i \beta_i}, \quad i = 1, 2.$$

Provided competition coefficients are patch dependent, Cressman et al. (2004) showed that infinitely fast adaptive dispersal can destabilize an otherwise stable interior equilibrium. However, they also showed that this can happen only if competition is patch dependent. The above methods can be used to extend these results to situations where demographic and dispersal dynamics operate on similar time scales. Using their example, Fig. 4 shows the situation where $A < 0, B < 0$ and $A + B > C + D$, i.e., where conditions of Proposition 2 for local equilibrium stability do not hold. Then, for small dispersal rates, the interior equilibrium is still locally asymptotically stable,

but becomes unstable due to a Hopf bifurcation for larger rates of dispersal. In fact, the simulations show that with increasing dispersal rates the amplitude of the cycle rapidly expands and along the cycle population densities become very close to zero (see also [Abrams et al. 2007](#)).

Such examples illustrate a new that the effects of time scales between ecological and behavioral processes cannot be ignored, especially for systems involving competing species.

5 Discussion

In this article, the effect of adaptive dispersal on population stability is investigated in a two patch environment. We showed that, when there is an equilibrium in each patch without dispersal and net dispersal between the two patches is in the direction of higher fitness, this remains an equilibrium in the resultant population–dispersal dynamics. The question of most interest is then how the stability of this equilibrium depends on the dispersal rates between patches.

Our results are most clear for a single species with individual fitness in each patch decreasing with population size. Here, within-patch population dynamics and adaptive dispersal will both lead the system to carrying capacity in each patch (Sect. 2). Thus, a population equilibrium with isolated patches (no dispersal) is globally asymptotically stable if and only if it is globally asymptotically stable for each choice of dispersal rates under the population–dispersal dynamics based on adaptive dispersal. To rephrase, adaptive dynamics does not affect the eventual outcome of such systems. We also show that passive dispersal leads to a locally asymptotically stable equilibrium that typically depends on the fixed dispersal rates. In particular, there will be under-matching (e.g., [Kennedy and Gray 1993](#)) in some patch where equilibrium density is below carrying capacity.

The effect of adaptive dispersal on two-species systems is more subtle and depends on the type of trophic interactions. When there are locally stable coexistence equilibria of predators and prey in each isolated patch (e.g., the Lotka–Volterra model), dispersal cannot destabilize the system (Proposition 1, Sect. 3). Conversely, when predator–prey population dynamics fluctuate (e.g., in the Rosenzweig–MacArthur model) in both isolated patches, we proved that adaptive dispersal cannot stabilize such unstable population dynamics. Thus, if the equilibrium in each patch is stable (respectively, unstable) without dispersal, then the inclusion of dispersal cannot change the stability (respectively, instability) of the equilibrium. However, large adaptive dispersal rates can lead to stability in overall predator–prey population densities provided population dynamics in only one patch are locally stable.

In the case of two competing species, a locally stable equilibrium without dispersal requires that interspecific competition is weaker than intraspecific competition in each patch. In the presence of adaptive dispersal, we showed that similar conditions involving virtual inter- and intra-specific competition between species in different patches must also be considered in order to analyze the stability of an interior equilibrium (Proposition 2, Sect. 4). In the special case of patch independent competition, dispersal does not alter the stability properties of this equilibrium. Furthermore, if the combined

interspecific virtual competition between patches is weaker than intraspecific virtual competition, then dispersal cannot destabilize an otherwise stable equilibrium. However, strong interspecific virtual competition effects can destabilize such an equilibrium when dispersal rates are sufficiently high.

The above results extend those of other studies on the effects of dispersal on population dynamics in multi-patch environments. These studies initially focused on a system where population dynamics are the same across patches and dispersal is random (e.g., Turing 1952; Levin 1974; Rohani and Ruxton 1999b). In this case, the equilibrium of the system without dispersal continues to be an equilibrium with dispersal and so the effect of dispersal on the equilibrium stability can be examined. These studies show that semi-antagonistic interactions (i.e., predator–prey type interactions) are necessary for dispersal induced instabilities to occur. Rohani and Ruxton (1999b) summarized the outcome of several studies on density-independent (i.e., passive) dispersal both in continuous and discrete space as follows: (a) if the individual populations are intrinsically unstable then dispersal cannot be stabilizing, (b) dispersal can only be destabilizing in predator–prey like systems and then only if the difference in dispersal rates for the two species is large. These results relate only to the case of the spatially homogeneous equilibrium (either in continuous space, or across patches).

The homogeneous equilibrium disappears when passive dispersal is non-random. In this case, the new resulting population equilibrium and its stability will depend on dispersal probabilities between patches and it is possible that intermediate dispersal rates will stabilize inherently unstable population dynamics (Hassell et al. 1991). A similar situation arises for the non homogeneous equilibrium that emerges when population dynamics are patch specific (Holt 1984, 1985; Murdoch et al. 2003). The models we have studied in this article are similar to the homogeneous case with random dispersal, even though population dynamics may be patch dependent, since the equilibrium is again independent of adaptive dispersal. That is, population-dispersal dynamics with density-dependent adaptive dispersal have the same population equilibrium as the corresponding system without dispersal.

In our models, we have focused on how stability of our dispersal-independent equilibrium depends on dispersal. When compared to studies on random dispersal, there is no destabilization due to adaptive dispersal in the predator–prey model. In other words, any diffusion driven Turing type instability is impossible when dispersal is adaptive. On the other hand, adaptive dispersal can lead to instability of the dispersal-independent equilibrium when the species are competitors, in contrast to those studies that assume random dispersal for competing species (Rohani and Ruxton 1999b). To exclude this possibility, one needs to assume not only that the intraspecific competition in each patch is stronger than interspecific competition, but also that the same condition holds for the virtual competition between species in different patches. Although the species do not literally compete in a virtual fashion, the effects of within-patch competition are felt across patches by means of the dispersal mechanism. This phenomenon is reminiscent of the “ghost of the competition past”, where two species are kept segregated in two different habitats as the result of their virtual (past) competition (Morris 1999).

Our results on population-dispersal stability of the predator–prey and competition models with adaptive dispersal were obtained using the linearization method and are

thus only local. Whether or not the asymptotic stability of the population-dispersal equilibrium is global, remains an open problem. In this article, we have assumed that adaptive dispersal implies net movement to the patch with the higher per capita growth rate. Our results do not necessarily extend to models where movement depends on other mechanisms (e.g., only on the growth rate in the current patch such as the partially adaptive model of Huang and Diekmann 2003). In particular, the equilibrium without dispersal may change under this type of movement.

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Appendix A: Stability of the interior equilibrium for the single-species patch model

First we consider the single species model (1) with fixed, density independent dispersal rates. Our model with positive carrying capacities has an interior equilibrium (Hofbauer and Sigmund 1998). The Jacobian matrix evaluated at the interior equilibrium is

$$J = \begin{pmatrix} f_1 + x_1 f_1' - d_{12}\delta & d_{21}\delta \\ d_{12}\delta & f_2 + x_2 f_2' - d_{21}\delta \end{pmatrix} = \begin{pmatrix} x_1 f_1' - d_{21} \frac{x_2}{x_1} \delta & d_{21}\delta \\ d_{12}\delta & x_2 f_2' - d_{12} \frac{x_1}{x_2} \delta \end{pmatrix}.$$

As we assume $f_i' < 0$, the trace of matrix J is negative and

$$\det J = x_1 x_2 f_1' f_2' - \delta d_{12} f_1' \frac{x_1^2}{x_2} - \delta d_{21} f_2' \frac{x_2^2}{x_1}$$

is positive. Thus, the interior equilibrium, is locally asymptotically stable independently of dispersal speed. In fact, it is globally asymptotically stable (Takeuchi 1996).

Now we consider the model where distribution dynamics are described by model (4). The Jacobian matrix evaluated at the carrying capacity K_i in each patch is

$$J = \begin{pmatrix} (K_1 + D(K_1, K_2))f_1'(K_1) & -D(K_1, K_2)f_2'(K_2) \\ -D(K_1, K_2)f_1'(K_1) & (K_2 + D(K_1, K_2))f_2'(K_2) \end{pmatrix}.$$

Since $f_i'(K_i) < 0$, the trace of matrix J is negative and

$$\det J = (K_1 K_2 + (K_1 + K_2)D(K_1, K_2))f_1'(K_1)f_2'(K_2)$$

is positive. Thus, the interior equilibrium is locally asymptotically stable independently of dispersal speed.

In fact, this equilibrium is globally asymptotically stable for any number of patches under adaptive dispersal because, if $\max_i f_i > 0$, then the patch (or patches) with highest payoff will increase in density both through within patch population growth and through a net gain from dispersal. By doing so, patch payoffs will necessarily decrease, i.e., $\max_i f_i$ is a decreasing function. Similarly, if $\min_i f_i < 0$, then $\min_i f_i$ is an increasing function. Therefore, $f_i \rightarrow 0$ for all i . This argument follows from the Lyapunov-like function method used by [Cressman and Křivan \(2006\)](#) (Appendix B) generalized to population-dispersal dynamics when dispersal is adaptive.

Appendix B: Stability of the interior equilibrium for predator–prey model (8)

The Jacobian at the interior equilibrium of model (8) [that we denote here as (x_1, x_2, y_1, y_2) for the sake of simplicity instead of $(x_1^*, x_2^*, y_1^*, y_2^*)$] is

$$\begin{pmatrix} (x_1 + D_x) \frac{\partial f_1}{\partial x_1} & -D_x \frac{\partial f_2}{\partial x_2} & (x_1 + D_x) \frac{\partial f_1}{\partial y_1} & -D_x \frac{\partial f_2}{\partial y_2} \\ -D_x \frac{\partial f_1}{\partial x_1} & (x_2 + D_x) \frac{\partial f_2}{\partial x_2} & -D_x \frac{\partial f_1}{\partial y_1} & (x_2 + D_x) \frac{\partial f_2}{\partial y_2} \\ (y_1 + D_y) g'_1 & -D_y g'_2 & 0 & 0 \\ -D_y g'_1 & (y_2 + D_y) g'_2 & 0 & 0 \end{pmatrix}$$

where D_x and D_y are the prey and predator dispersal rates respectively evaluated at this equilibrium.

The coefficients of the characteristic polynomial $\lambda^4 + A_1\lambda^3 + A_2\lambda^2 + A_3\lambda + A_4$ are

$$\begin{aligned} A_1 &= -(x_1 + D_x) \frac{\partial f_1}{\partial x_1} - (x_2 + D_x) \frac{\partial f_2}{\partial x_2}, \\ A_2 &= -g'_1 \left((D_x + x_1)(D_y + y_1) \frac{\partial f_1}{\partial y_1} + D_x D_y \frac{\partial f_2}{\partial y_2} \right) \\ &\quad - g'_2 \left(D_x D_y \frac{\partial f_1}{\partial y_1} + (D_x + x_2)(D_y + y_2) \frac{\partial f_2}{\partial y_2} \right) \\ &\quad + (x_1 x_2 + D_x(x_1 + x_2)) \frac{\partial f_1}{\partial x_1} \frac{\partial f_2}{\partial x_2}, \\ A_3 &= (x_1 x_2 + D_x(x_1 + x_2)) \left((D_y + y_1) g'_1 \frac{\partial f_1}{\partial y_1} \frac{\partial f_2}{\partial x_2} + (D_y + y_2) g'_2 \frac{\partial f_1}{\partial x_1} \frac{\partial f_2}{\partial y_2} \right), \\ A_4 &= g'_1 g'_2 (x_1 x_2 + D_x(x_1 + x_2)) (y_1 y_2 + D_y(y_1 + y_2)) \frac{\partial f_1}{\partial y_1} \frac{\partial f_2}{\partial y_2}. \end{aligned}$$

By the Routh–Hurwitz conditions for 4×4 matrices ([Allen 2007](#)), all eigenvalues of the Jacobian have negative real parts if and only if all A_i 's are positive and

$$A_3(A_1 A_2 - A_3) - A_1^2 A_4 > 0. \tag{16}$$

Clearly, by our assumptions on f_i and g_i , all A_i 's are positive. To prove (16), we first show that $A_1A_2 - A_3 > 0$.

$$\begin{aligned}
 A_1A_2 - A_3 &= \left((x_1 + D_x) \frac{\partial f_1}{\partial x_1} + (x_2 + D_x) \frac{\partial f_2}{\partial x_2} \right) \\
 &\quad \times \left(g'_1 \left((D_x + x_1)(D_y + y_1) \frac{\partial f_1}{\partial y_1} + D_x D_y \frac{\partial f_2}{\partial y_2} \right) \right. \\
 &\quad \left. + g'_2 \left(D_x D_y \frac{\partial f_1}{\partial y_1} + (D_x + x_2)(D_y + y_2) \frac{\partial f_2}{\partial y_2} \right) \right. \\
 &\quad \left. - (x_1x_2 + D_x(x_1 + x_2)) \frac{\partial f_1}{\partial x_1} \frac{\partial f_2}{\partial x_2} \right) \\
 &\quad - (x_1x_2 + D_x(x_1 + x_2)) \left((D_y + y_1)g'_1 \frac{\partial f_1}{\partial y_1} \frac{\partial f_2}{\partial x_2} + (D_y + y_2)g'_2 \frac{\partial f_1}{\partial x_1} \frac{\partial f_2}{\partial y_2} \right) \\
 &= \left((x_1 + D_x) \frac{\partial f_1}{\partial x_1} + (x_2 + D_x) \frac{\partial f_2}{\partial x_2} \right) \left(g'_1(D_x + x_1)(D_y + y_1) \frac{\partial f_1}{\partial y_1} \right. \\
 &\quad \left. + g'_2(D_x + x_2)(D_y + y_2) \frac{\partial f_2}{\partial y_2} \right) \\
 &\quad + \left((x_1 + D_x) \frac{\partial f_1}{\partial x_1} + (x_2 + D_x) \frac{\partial f_2}{\partial x_2} \right) \left(g'_1 \frac{\partial f_2}{\partial y_2} + g'_2 \frac{\partial f_1}{\partial y_1} \right) D_x D_y \\
 &\quad - (x_1x_2 + D_x(x_1 + x_2)) \left((x_1 + D_x) \frac{\partial f_1}{\partial x_1} + (x_2 + D_x) \frac{\partial f_2}{\partial x_2} \right) \frac{\partial f_1}{\partial x_1} \frac{\partial f_2}{\partial x_2} \\
 &\quad - (x_1x_2 + D_x(x_1 + x_2)) \left((D_y + y_1)g'_1 \frac{\partial f_1}{\partial y_1} \frac{\partial f_2}{\partial x_2} + (D_y + y_2)g'_2 \frac{\partial f_1}{\partial x_1} \frac{\partial f_2}{\partial y_2} \right). \tag{17}
 \end{aligned}$$

Since

$$-(x_1(D_x + x_2) + D_x x_2) \left((x_1 + D_x) \frac{\partial f_1}{\partial x_1} + (x_2 + D_x) \frac{\partial f_2}{\partial x_2} \right) \frac{\partial f_1}{\partial x_1} \frac{\partial f_2}{\partial x_2}$$

and

$$\left((x_1 + D_x) \frac{\partial f_1}{\partial x_1} + (x_2 + D_x) \frac{\partial f_2}{\partial x_2} \right) \left(g'_1 \frac{\partial f_2}{\partial y_2} + g'_2 \frac{\partial f_1}{\partial y_1} \right) D_x D_y$$

are positive, $A_1A_2 - A_3$ is greater than expression (17) with these terms deleted. It is also greater than the expression resulting from deleting these terms and replacing $x_1x_2 + D_x(x_1 + x_2)$ by $(x_1 + D_x)(x_2 + D_x)$ in expression (17). Thus, we get

$$\begin{aligned}
 A_1 A_2 - A_3 &> \left((x_1 + D_x) \frac{\partial f_1}{\partial x_1} + (x_2 + D_x) \frac{\partial f_2}{\partial x_2} \right) \\
 &\quad \times \left(g'_1 (D_x + x_1) (D_y + y_1) \frac{\partial f_1}{\partial y_1} + g'_2 (D_x + x_2) (D_y + y_2) \frac{\partial f_2}{\partial y_2} \right) \\
 &\quad - (x_1 + D_x) (x_2 + D_x) \left((D_y + y_1) g'_1 \frac{\partial f_1}{\partial y_1} \frac{\partial f_2}{\partial x_2} + (D_y + y_2) g'_2 \frac{\partial f_1}{\partial x_1} \frac{\partial f_2}{\partial y_2} \right) \\
 &= (x_1 + D_x)^2 (y_1 + D_y) g'_1 \frac{\partial f_1}{\partial x_1} \frac{\partial f_1}{\partial y_1} + (x_2 + D_x)^2 (y_2 + D_y) g'_2 \frac{\partial f_2}{\partial x_2} \frac{\partial f_2}{\partial y_2} \geq 0.
 \end{aligned}$$

Moreover,

$$A_4 \leq g'_1 g'_2 (x_1 (x_2 + D_x) + D_x x_2) (y_1 + D_y) (y_2 + D_y) \frac{\partial f_1}{\partial y_1} \frac{\partial f_2}{\partial y_2},$$

and so

$$\begin{aligned}
 A_1^2 A_4 &< \left((x_1 + D_x) \frac{\partial f_1}{\partial x_1} + (x_2 + D_x) \frac{\partial f_2}{\partial x_2} \right)^2 \\
 &\quad \times g'_1 g'_2 (x_1 (x_2 + D_x) + D_x x_2) (y_1 + D_y) (y_2 + D_y) \frac{\partial f_1}{\partial y_1} \frac{\partial f_2}{\partial y_2}.
 \end{aligned}$$

It follows that

$$\begin{aligned}
 A_3 (A_1 A_2 - A_3) - A_1^2 A_4 &> (x_1 (D_x + x_2) + D_x x_2) \\
 &\quad \times \left((D_y + y_1) g'_1 \frac{\partial f_1}{\partial y_1} \frac{\partial f_2}{\partial x_2} + (D_y + y_2) g'_2 \frac{\partial f_1}{\partial x_1} \frac{\partial f_2}{\partial y_2} \right) \\
 &\quad \times \left((x_1 + D_x)^2 (y_1 + D_y) g'_1 \frac{\partial f_1}{\partial x_1} \frac{\partial f_1}{\partial y_1} + (x_2 + D_x)^2 (y_2 + D_y) g'_2 \frac{\partial f_2}{\partial x_2} \frac{\partial f_2}{\partial y_2} \right) \\
 &\quad - \left((x_1 + D_x) \frac{\partial f_1}{\partial x_1} + (x_2 + D_x) \frac{\partial f_2}{\partial x_2} \right)^2 g'_1 g'_2 (x_1 (x_2 + D_x) \\
 &\quad + D_x x_2) (y_1 + D_y) (y_2 + D_y) \frac{\partial f_1}{\partial y_1} \frac{\partial f_2}{\partial y_2} \\
 &= (x_1 (x_2 + D_x) + D_x x_2) \frac{\partial f_1}{\partial x_1} \frac{\partial f_2}{\partial x_2} \left(\frac{\partial f_1}{\partial y_1} (x_1 + D_x) (y_1 + D_y) g'_1 \right. \\
 &\quad \left. - \frac{\partial f_2}{\partial y_2} (x_2 + D_x) (y_2 + D_y) g'_2 \right)^2 \geq 0.
 \end{aligned}$$

We also observe that in the case of the Holling type II functional response when predator–prey population dynamics are unstable in both patches (which happens when $\frac{\partial f_1}{\partial x_1} > 0, \frac{\partial f_2}{\partial x_2} > 0$) coefficient A_1 is negative and the population equilibrium is unstable. In the mixed case when predator–prey population dynamics are unstable in one patch but stable in the other patch (which happens when $\frac{\partial f_1}{\partial x_1} > 0, \frac{\partial f_2}{\partial x_2} < 0$ or vice versa), we cannot use the above analysis to infer local stability of the population equilibrium independently of dispersal rates. Numerical simulations (such as those in

Fig. 3, bottom panels) show that large enough dispersal rates can stabilize population dynamics.

Appendix C: Routh–Hurwitz stability condition for the competition model

The Jacobian at the equilibrium of model (14) is

$$\begin{pmatrix} (x_1 + D_x) \frac{\partial f_1}{\partial x_1} & -D_x \frac{\partial f_2}{\partial x_2} & (x_1 + D_x) \frac{\partial f_1}{\partial y_1} & -D_x \frac{\partial f_2}{\partial y_2} \\ -D_x \frac{\partial f_1}{\partial x_1} & (x_2 + D_x) \frac{\partial f_2}{\partial x_2} & -D_x \frac{\partial f_1}{\partial y_1} & (x_2 + D_x) \frac{\partial f_2}{\partial y_2} \\ (y_1 + D_y) \frac{\partial g_1}{\partial x_1} & -D_y \frac{\partial g_2}{\partial x_2} & (y_1 + D_y) \frac{\partial g_1}{\partial y_1} & -D_y \frac{\partial g_2}{\partial y_2} \\ -D_y \frac{\partial g_1}{\partial x_1} & (y_2 + D_y) \frac{\partial g_2}{\partial x_2} & -D_y \frac{\partial g_1}{\partial y_1} & (y_2 + D_y) \frac{\partial g_2}{\partial y_2} \end{pmatrix}.$$

In what follows we set

$$\begin{aligned} A &= \frac{\partial f_1}{\partial y_1} \frac{\partial g_1}{\partial x_1} - \frac{\partial f_1}{\partial x_1} \frac{\partial g_1}{\partial y_1}, \\ B &= \frac{\partial f_2}{\partial y_2} \frac{\partial g_2}{\partial x_2} - \frac{\partial f_2}{\partial x_2} \frac{\partial g_2}{\partial y_2}, \\ C &= \frac{\partial f_1}{\partial x_1} \frac{\partial g_2}{\partial y_2} - \frac{\partial f_1}{\partial y_1} \frac{\partial g_2}{\partial x_2}, \\ D &= \frac{\partial f_2}{\partial x_2} \frac{\partial g_1}{\partial y_1} - \frac{\partial f_2}{\partial y_2} \frac{\partial g_1}{\partial x_1}, \\ X &= D_x(x_1 + x_2) + x_1x_2 > 0, \\ Y &= D_y(y_1 + y_2) + y_1y_2 > 0. \end{aligned}$$

We also use the following inequalities

$$X \leq (D_x + x_1)(D_x + x_2), \quad Y \leq (D_y + y_1)(D_y + y_2).$$

The coefficients of the characteristic polynomial $\lambda^4 + A_1\lambda^3 + A_2\lambda^2 + A_3\lambda + A_4$ are

$$\begin{aligned} A_1 &= -(D_x + x_1) \frac{\partial f_1}{\partial x_1} - (D_x + x_2) \frac{\partial f_2}{\partial x_2} - (D_y + y_1) \frac{\partial g_1}{\partial y_1} - (D_y + y_2) \frac{\partial g_2}{\partial y_2}, \\ A_2 &= X \frac{\partial f_1}{\partial x_1} \frac{\partial f_2}{\partial x_2} - (x_1 + D_x)(y_1 + D_y)A \\ &\quad + (x_1 + D_x)(y_2 + D_y) \frac{\partial f_1}{\partial x_1} \frac{\partial g_2}{\partial y_2} - D_x D_y \frac{\partial f_2}{\partial y_2} \frac{\partial g_1}{\partial x_1} \end{aligned}$$

$$\begin{aligned}
 &+Y \frac{\partial g_1}{\partial y_1} \frac{\partial g_2}{\partial y_2} - (x_2 + D_x)(y_2 + D_y)B + (x_2 + D_x)(y_1 + D_y) \frac{\partial f_2}{\partial x_2} \frac{\partial g_1}{\partial y_1} \\
 &-D_x D_y \frac{\partial f_1}{\partial y_1} \frac{\partial g_2}{\partial x_2}, \\
 A_3 = &\left(\frac{\partial g_2}{\partial y_2} (D_x + x_1)Y + \frac{\partial f_2}{\partial x_2} (D_y + y_1)X \right) A \\
 &+ \left(\frac{\partial g_1}{\partial y_1} (D_x + x_2)Y + \frac{\partial f_1}{\partial x_1} (D_y + y_2)X \right) B,
 \end{aligned}$$

and

$$A_4 = XYAB.$$

Assuming that $\frac{\partial f_1}{\partial x_1} < 0$, $\frac{\partial f_2}{\partial x_2} < 0$, $\frac{\partial g_1}{\partial y_1} < 0$, $\frac{\partial g_2}{\partial y_2} < 0$, $A < 0$, and $B < 0$, then A_i is positive for $i = 1, 3, 4$. The $D_x D_y$ term of A_2 has coefficient

$$-A - B + C + D.$$

This could be negative, in which case the equilibrium will be unstable when D_x and D_y are large enough. This proves that condition $C + D > A + B$ from Proposition 2 is a necessary condition for local stability of the interior equilibrium to be independent of dispersal rates. In particular, if $C + D > A + B$, then $A_2 > 0$ since all of its other terms are positive.

Now assume that $C + D > 0$ (and A, B are negative). Then

$$\begin{aligned}
 A_2 \geq &X \frac{\partial f_1}{\partial x_1} \frac{\partial f_2}{\partial x_2} - (x_1 + D_x)(y_1 + D_y)A + (x_1 y_2 + D_x y_2 + D_y x_1) \frac{\partial f_1}{\partial x_1} \frac{\partial g_2}{\partial y_2} \\
 &+Y \frac{\partial g_1}{\partial y_1} \frac{\partial g_2}{\partial y_2} - (x_2 + D_x)(y_2 + D_y)B + (x_2 y_1 + D_x y_1 + D_y x_2) \frac{\partial f_2}{\partial x_2} \frac{\partial g_1}{\partial y_1}.
 \end{aligned}$$

Using the above lower estimate of A_2 yields

$$\begin{aligned}
 A_1 A_2 - A_3 \geq &-\left[(x_1 + D_x) \frac{\partial f_1}{\partial x_1} + (x_2 + D_x) \frac{\partial f_2}{\partial x_2} + (y_1 + D_y) \frac{\partial g_1}{\partial y_1} \right. \\
 &\left. + (y_2 + D_y) \frac{\partial g_2}{\partial y_2} \right] \left[X \frac{\partial f_1}{\partial x_1} \frac{\partial f_2}{\partial x_2} + (x_1 y_2 + D_x y_2 + D_y x_1) \frac{\partial f_1}{\partial x_1} \frac{\partial g_2}{\partial y_2} \right. \\
 &\left. + Y \frac{\partial g_1}{\partial y_1} \frac{\partial g_2}{\partial y_2} + (x_2 y_1 + D_x y_1 + D_y x_2) \frac{\partial f_2}{\partial x_2} \frac{\partial g_1}{\partial y_1} \right] \\
 &+ \left[(x_1 + D_x) \frac{\partial f_1}{\partial x_1} + (y_1 + D_y) \frac{\partial g_1}{\partial y_1} \right] (x_1 + D_x)(y_1 + D_y)A \\
 &+ \left[(x_2 + D_x) \frac{\partial f_2}{\partial x_2} + (y_2 + D_y) \frac{\partial g_2}{\partial y_2} \right] (x_2 + D_x)(y_2 + D_y)B
 \end{aligned}$$

$$\begin{aligned}
& +(y_1 + D_y) \frac{\partial f_2}{\partial x_2} A D_x^2 + (x_1 + D_x) \frac{\partial g_2}{\partial y_2} A D_y^2 \\
& +(y_2 + D_y) \frac{\partial f_1}{\partial x_1} B D_x^2 + (x_2 + D_x) \frac{\partial g_1}{\partial y_1} B D_y^2 \\
> & - \left[(x_1 + D_x) \frac{\partial f_1}{\partial x_1} + (x_2 + D_x) \frac{\partial f_2}{\partial x_2} + (y_1 + D_y) \frac{\partial g_1}{\partial y_1} \right. \\
& \left. + (y_2 + D_y) \frac{\partial g_2}{\partial y_2} \right] \left[X \frac{\partial f_1}{\partial x_1} \frac{\partial f_2}{\partial x_2} + Y \frac{\partial g_1}{\partial y_1} \frac{\partial g_2}{\partial y_2} \right] \\
& + \left[(x_1 + D_x) \frac{\partial f_1}{\partial x_1} + (y_1 + D_y) \frac{\partial g_1}{\partial y_1} \right] (x_1 + D_x)(y_1 + D_y) A \\
& + \left[(x_2 + D_x) \frac{\partial f_2}{\partial x_2} + (y_2 + D_y) \frac{\partial g_2}{\partial y_2} \right] (x_2 + D_x)(y_2 + D_y) B \\
> & 0.
\end{aligned}$$

We observe that

$$\begin{aligned}
& - \left[(x_1 + D_x) \frac{\partial f_1}{\partial x_1} + (x_2 + D_x) \frac{\partial f_2}{\partial x_2} + (y_1 + D_y) \frac{\partial g_1}{\partial y_1} \right. \\
& \left. + (y_2 + D_y) \frac{\partial g_2}{\partial y_2} \right] \left[X \frac{\partial f_1}{\partial x_1} \frac{\partial f_2}{\partial x_2} + Y \frac{\partial g_1}{\partial y_1} \frac{\partial g_2}{\partial y_2} \right] \\
= & - \left(\frac{\partial f_1}{\partial x_1} \right)^2 \frac{\partial f_2}{\partial x_2} X (x_1 + D_x) \\
& - \frac{\partial f_1}{\partial x_1} \left(\frac{\partial f_2}{\partial x_2} \right)^2 X (x_2 + D_x) - \left(\frac{\partial g_1}{\partial y_1} \right)^2 \frac{\partial g_2}{\partial y_2} Y (y_1 + D_y) \\
& - \frac{\partial g_1}{\partial y_1} \left(\frac{\partial g_2}{\partial y_2} \right)^2 Y (y_2 + D_y) - \frac{\partial f_2}{\partial x_2} \frac{\partial g_1}{\partial y_1} \frac{\partial g_2}{\partial y_2} Y (x_2 + D_x) \\
& - \frac{\partial f_1}{\partial x_1} \frac{\partial g_1}{\partial y_1} \frac{\partial g_2}{\partial y_2} Y (x_1 + D_x) - \frac{\partial f_1}{\partial x_1} \frac{\partial f_2}{\partial x_2} \frac{\partial g_1}{\partial y_1} X (y_1 + D_y) \\
& - \frac{\partial f_1}{\partial x_1} \frac{\partial f_2}{\partial x_2} \frac{\partial g_2}{\partial y_2} X (y_2 + D_y) > A X (y_1 + D_y) \frac{\partial f_2}{\partial x_2} + B X (y_2 + D_y) \frac{\partial f_1}{\partial x_1} \\
& + A Y (x_1 + D_x) \frac{\partial g_2}{\partial y_2} + B Y (x_2 + D_x) \frac{\partial g_1}{\partial x_1} = A_3.
\end{aligned}$$

In the last inequality, we ignored all terms that contain a squared partial derivative and used the fact that $-\frac{\partial f_1}{\partial x_1} \frac{\partial g_1}{\partial y_1} < A$ and $-\frac{\partial f_2}{\partial x_2} \frac{\partial g_2}{\partial y_2} < B$.

The above calculations prove the following result.

Proposition 3

$$A_1 A_2 - A_3 > A_3 + \left((D_x + x_1) \frac{\partial f_1}{\partial x_1} + (D_y + y_1) \frac{\partial g_1}{\partial y_1} \right) (D_x + x_1)(D_y + y_1)A + \left((D_x + x_2) \frac{\partial f_2}{\partial x_2} + (D_y + y_2) \frac{\partial g_2}{\partial y_2} \right) (D_x + x_2)(D_y + y_2)B.$$

Using these inequalities we now prove that $A_3(A_1 A_2 - A_3) - A_1^2 A_4 > 0$. We have

$$\begin{aligned} & A_3(A_1 A_2 - A_3) - A_1^2 A_4 \\ & > A_3^2 + \left[\left(\frac{\partial g_2}{\partial y_2} (D_x + x_1)Y + \frac{\partial f_2}{\partial x_2} (D_y + y_1)X \right) A + \left(\frac{\partial g_1}{\partial y_1} (D_x + x_2)Y + \frac{\partial f_1}{\partial x_1} (D_y + y_2)X \right) B \right] \\ & \times \left[\left((D_x + x_1) \frac{\partial f_1}{\partial x_1} + (D_y + y_1) \frac{\partial g_1}{\partial y_1} \right) (D_x + x_1)(D_y + y_1)A + \left((D_x + x_2) \frac{\partial f_2}{\partial x_2} + (D_y + y_2) \frac{\partial g_2}{\partial y_2} \right) (D_x + x_2)(D_y + y_2)B \right] \\ & - \left((D_x + x_1) \frac{\partial f_1}{\partial x_1} + (D_x + x_2) \frac{\partial f_2}{\partial x_2} + (D_y + y_1) \frac{\partial g_1}{\partial y_1} + (D_y + y_2) \frac{\partial g_2}{\partial y_2} \right)^2 ABXY = A_3^2 \\ & + A^2 \left(\frac{\partial g_2}{\partial y_2} (D_x + x_1)Y + \frac{\partial f_2}{\partial x_2} (D_y + y_1)X \right) \\ & \times \left((D_x + x_1) \frac{\partial f_1}{\partial x_1} + (D_y + y_1) \frac{\partial g_1}{\partial y_1} \right) (D_x + x_1)(D_y + y_1) \\ & + B^2 \left(\frac{\partial g_1}{\partial y_1} (D_x + x_2)Y + \frac{\partial f_1}{\partial x_1} (D_y + y_2)X \right) \\ & \times \left((D_x + x_2) \frac{\partial f_2}{\partial x_2} + (D_y + y_2) \frac{\partial g_2}{\partial y_2} \right) (D_x + x_2)(D_y + y_2) \\ & + AB \left[\left(\frac{\partial g_2}{\partial y_2} (D_x + x_1)Y + \frac{\partial f_2}{\partial x_2} (D_y + y_1)X \right) \left((D_x + x_2) \frac{\partial f_2}{\partial x_2} + (D_y + y_2) \frac{\partial g_2}{\partial y_2} \right) (D_x + x_2)(D_y + y_2) \right. \\ & \left. + \left(\frac{\partial g_1}{\partial y_1} (D_x + x_2)Y + \frac{\partial f_1}{\partial x_1} (D_y + y_2)X \right) \right. \\ & \left. \times \left((D_x + x_1) \frac{\partial f_1}{\partial x_1} + (D_y + y_1) \frac{\partial g_1}{\partial y_1} \right) (D_x + x_1)(D_y + y_1) \right] \end{aligned}$$

$$\begin{aligned}
& - \left[(D_x + x_1) \frac{\partial f_1}{\partial x_1} + (D_x + x_2) \frac{\partial f_2}{\partial x_2} + (D_y + y_1) \frac{\partial g_1}{\partial y_1} \right. \\
& \left. + (D_y + y_2) \frac{\partial g_2}{\partial y_2} \right]^2 XY \Big] = A_3^2 \\
& + A^2 \left(\frac{\partial g_2}{\partial y_2} (D_x + x_1) Y + \frac{\partial f_2}{\partial x_2} (D_y + y_1) X \right) \\
& \times \left((D_x + x_1) \frac{\partial f_1}{\partial x_1} + (D_y + y_1) \frac{\partial g_1}{\partial y_1} \right) (D_x + x_1) (D_y + y_1) \\
& + B^2 \left(\frac{\partial g_1}{\partial y_1} (D_x + x_2) Y + \frac{\partial f_1}{\partial x_1} (D_y + y_2) X \right) \\
& \times \left((D_x + x_2) \frac{\partial f_2}{\partial x_2} + (D_y + y_2) \frac{\partial g_2}{\partial y_2} \right) (D_x + x_2) (D_y + y_2) \\
& + AB \left(\left(\frac{\partial g_2}{\partial y_2} \right)^2 (D_y + y_2)^2 Y D_x^2 + \left(\frac{\partial f_2}{\partial x_2} \right)^2 (D_x + x_2)^2 X D_y^2 \right. \\
& + \left. \left(\frac{\partial f_1}{\partial x_1} \right)^2 (D_x + x_1)^2 X D_y^2 + \left(\frac{\partial g_1}{\partial y_1} \right)^2 (D_y + y_1)^2 Y D_x^2 \right. \\
& + \frac{\partial f_2}{\partial x_2} \frac{\partial g_2}{\partial y_2} (D_x + x_2) (D_y + y_2) (D_x^2 Y + D_y^2 X) \\
& + \left. \frac{\partial f_1}{\partial x_1} \frac{\partial g_1}{\partial y_1} (D_x + x_1) (D_y + y_1) (D_x^2 Y + D_y^2 X) \right. \\
& - 2(D_x + x_1)(D_x + x_2) \frac{\partial f_1}{\partial x_1} \frac{\partial f_2}{\partial x_2} XY - 2(D_x + x_1)(D_y + y_2) \frac{\partial f_1}{\partial x_1} \frac{\partial g_2}{\partial y_2} XY \\
& \left. - 2(D_x + x_2)(D_y + y_1) \frac{\partial f_2}{\partial x_2} \frac{\partial g_1}{\partial y_1} XY - 2(D_y + y_1)(D_y + y_2) \frac{\partial g_1}{\partial y_1} \frac{\partial g_2}{\partial y_2} XY \right) = A_3^2 \\
& + \left(A^2 (D_x + x_1)^2 (D_y + y_1)^2 - 2(D_x + x_1)(D_x + x_2) Y A B \right. \\
& + (D_x + x_2)^2 (D_y + y_2)^2 B^2 \Big) X \frac{\partial f_1}{\partial x_1} \frac{\partial f_2}{\partial x_2} \\
& + \left(A^2 (D_x + x_1)^2 (D_y + y_1)^2 - 2(D_y + y_1)(D_y + y_2) X A B \right. \\
& + (D_x + x_2)^2 (D_y + y_2)^2 B^2 \Big) Y \frac{\partial g_1}{\partial y_1} \frac{\partial g_2}{\partial y_2} \\
& + \left(A^2 (D_x + x_1)^3 (D_y + y_1) Y - 2(D_x + x_1)(D_y + y_2) X Y A B \right. \\
& + (D_x + x_2)(D_y + y_2)^3 X B^2 \Big) \frac{\partial f_1}{\partial x_1} \frac{\partial g_2}{\partial y_2} \\
& + \left(A^2 (D_x + x_1)(D_y + y_1)^3 X - 2(D_x + x_2)(D_y + y_1) X Y A B \right. \\
& + (D_x + x_2)^3 (D_y + y_2) Y B^2 \Big) \frac{\partial f_2}{\partial x_2} \frac{\partial g_1}{\partial y_1}
\end{aligned}$$

$$\begin{aligned}
 &+AB \left(\left(\frac{\partial g_2}{\partial y_2}\right)^2 (D_y + y_2)^2 Y D_x^2 + \left(\frac{\partial f_2}{\partial x_2}\right)^2 (D_x + x_2)^2 X D_y^2 \right. \\
 &+ \left. \left(\frac{\partial f_1}{\partial x_1}\right)^2 (D_x + x_1)^2 X D_y^2 + \left(\frac{\partial g_1}{\partial y_1}\right)^2 (D_y + y_1)^2 Y D_x^2 + \frac{\partial f_2}{\partial x_2} \frac{\partial g_2}{\partial y_2} (D_x + x_2) \right. \\
 &\times \left. (D_y + y_2)(D_x^2 Y + D_y^2 X) + \frac{\partial f_1}{\partial x_1} \frac{\partial g_1}{\partial y_1} (D_x + x_1)(D_y + y_1)(D_x^2 Y + D_y^2 X) \right) > A_3^2 \\
 &+ (A(D_x + x_1)(D_y + y_1) - (D_x + x_2)(D_y + y_2)B)^2 X \frac{\partial f_1}{\partial x_1} \frac{\partial f_2}{\partial x_2} \\
 &+ (A(D_x + x_1)(D_y + y_1) - (D_x + x_2)(D_y + y_2)B)^2 Y \frac{\partial g_1}{\partial y_1} \frac{\partial g_2}{\partial y_2} \\
 &+ \left(A^2(D_x + x_1)^3 (D_y + y_1)Y - 2(D_x + x_1)(D_y + y_2)XYAB \right. \\
 &+ \left. (D_x + x_2)(D_y + y_2)^3 XB^2 \right) \frac{\partial f_1}{\partial x_1} \frac{\partial g_2}{\partial y_2} \\
 &+ \left(A^2(D_x + x_1)(D_y + y_1)^3 X - 2(D_x + x_2)(D_y + y_1)XYAB \right. \\
 &+ \left. (D_x + x_2)^3 (D_y + y_2)YB^2 \right) \frac{\partial f_2}{\partial x_2} \frac{\partial g_1}{\partial y_1}
 \end{aligned}$$

where in the last inequality we replaced Y by $(y_1 + D_y)(y_2 + D_y)$ and X by $(x_1 + D_x)(x_2 + D_x)$ in the first two terms. Because

$$\begin{aligned}
 A_3^2 &= \left(\frac{\partial g_1}{\partial y_1} (D_x + x_2)B + \frac{\partial g_2}{\partial y_2} (D_x + x_1)A \right)^2 Y^2 \\
 &+ \left(\frac{\partial f_1}{\partial x_1} (D_y + y_2)B + \frac{\partial f_2}{\partial x_2} (D_y + y_1)A \right)^2 X^2 \\
 &+ 2XY \left(A \frac{\partial g_2}{\partial y_2} (x_1 + D_x) + B \frac{\partial g_1}{\partial y_1} (x_2 + D_x) \right) \\
 &\times \left(A \frac{\partial f_2}{\partial x_2} (y_1 + D_y) + B \frac{\partial f_1}{\partial x_1} (y_2 + D_y) \right),
 \end{aligned}$$

we observe that

$$\begin{aligned}
 &A_3(A_1A_2 - A_3) - A_1^2A_4 \\
 &> (A(D_x + x_1)(D_y + y_1) - (D_x + x_2)(D_y + y_2)B)^2 X \frac{\partial f_1}{\partial x_1} \frac{\partial f_2}{\partial x_2} \\
 &+ (A(D_x + x_1)(D_y + y_1) - (D_x + x_2)(D_y + y_2)B)^2 Y \frac{\partial g_1}{\partial y_1} \frac{\partial g_2}{\partial y_2} > 0.
 \end{aligned}$$

This completes the proof of Proposition 2.

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