

# Spatially heterogeneous populations with mixed negative and positive local density dependence



Diana Knipl<sup>a,b,\*</sup>, Gergely Röst<sup>c</sup>

<sup>a</sup> Agent-Based Modelling Laboratory, York University, 331 Lumbers, 4700 Keele St., Toronto, Ontario M3J 1P3, Canada

<sup>b</sup> MTA–SZTE Analysis and Stochastic Research Group, University of Szeged, Aradi vértanúk tere 1, Szeged, H-6720, Hungary

<sup>c</sup> Bolyai Institute, University of Szeged, Aradi vértanúk tere 1, Szeged, H-6720, Hungary

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## ABSTRACT

Identifying the steady states of a population is a key issue in theoretical ecology, that includes the study of spatially heterogeneous populations. There are several examples of real ecosystems in patchy environments where the habitats are heterogeneous in their local density dependence. We investigate a multi-patch model of a single species with spatial dispersal, where the growth of the local population is logistic in some localities (negative density dependence) while other patches exhibit a strong Allee effect (positive density dependence). When the local dynamics is logistic in each patch and the habitats are interconnected by dispersal then the total population has only the extinction steady state and a componentwise positive equilibrium, corresponding to persistence in each patch. We show that animal populations in patchy environments can have a large number of steady states if local density dependence varies over the locations. It is demonstrated that, depending on the network topology of migration routes between the patches, the interaction of spatial dispersal and local density dependence can create a variety of coexisting stable positive equilibria. We give a detailed description of the multiple ways dispersal can rescue local populations from extinction.

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Population dynamics studies the changes over time in the size (density) of a group of individuals who share the same habitat. Since there are so many interactions between individuals and the environment, describing how populations grow or shrink is often a complex task. Mathematical growth models are frequently used to better understand these dynamics in real populations. In simplest terms, the change in the size of the population can be expressed by the difference of births and deaths. If environmental conditions are favourable (that is, food, space, etc. are abundant), then the population is able to grow. Growth is said to be exponential when the growth rate is proportional to the total population size. However, when resources are limited, an intraspecific competition of the individuals can occur which results in a slowdown of the exponential growth as competition for the resources increases.

*Abbreviations:* EAD, extinct in the absence of spatial dispersal; OAD, occupied in the absence of spatial dispersal.

\* Correspondence to: Department of Mathematics, University College London, Gower Street, London WC1E 6BT, United Kingdom.

E-mail addresses: [knipl@yorku.ca](mailto:knipl@yorku.ca), [d.knipl@ucl.ac.uk](mailto:d.knipl@ucl.ac.uk), [knipl@math.u-szeged.hu](mailto:knipl@math.u-szeged.hu) (D. Knipl), [rost@math.u-szeged.hu](mailto:rost@math.u-szeged.hu) (G. Röst).

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Eventually, population growth decreases nearly to zero as the population reaches the carrying capacity of the environment. This way, the growth of the population is described by an S-shaped curve, known as the logistic curve.

Numerous examples illustrate that in real ecosystems the growth of populations can exhibit another type of dynamics, the Allee effect, which is very different from that of exponential and logistic growth. Animal populations are often subject to the Allee effect, that is, they are better able to grow at higher densities. The concept was first described by Warder Clyde Allee, who studied the growth of goldfish. While classical population dynamics modelling approaches – including the concepts of exponential and logistic growth – assume negative density dependence of per capita growth rate, Allee's experiments showed that goldfish were better able to survive on higher densities. It has been observed that certain aquatic species can affect the chemistry of the water by releasing protective chemicals that could enhance their survival. In a tank, goldfish better manage to render the water closer to their optimal chemical requirements when there are several of them (Allee and Bowen, 1932). Based on his experiments and observations, Allee arrived to the conclusion that

the evolution of social structures is not only driven by competition (which classically implies negative density dependence), but that cooperation is another fundamental principle in animal species (Allee, 1931). The individuals of many species cooperate in various ways: they join forces to hunt or to escape predators, they forage together, they use cooperative strategies to survive unfavourable conditions, or they seek partners for reproduction.

The phenomenon of the Allee effect, often referred to as positive density dependence in population growth, has been studied comprehensively in the literature. Both in the direction of theoretical works with mathematical models and empirical works with the unveiling of Allee dynamics in natural populations, a large number of studies have been published (Dennis, 1989; Courchamp et al., 1999; Berec et al., 2007; Stephens and Sutherland, 1999). We also refer to the excellent book of Courchamp et al. (2008) which details the history and recent developments of the topic, and also provides a thorough overview of the relevant literature. We distinguish two types of Allee effect: the strong and the weak Allee effects. The strong Allee effect includes a population threshold that is often referred to as the Allee threshold: the population goes extinct when rare (per capita growth rate is negative), and it is able to grow at densities higher than the threshold (Dennis, 1989; Lewis and Kareiva, 1993; Odum and Barrett, 2004). In case when a weak Allee effect occurs in the population, the per capita population growth rate is lower (however, still positive) at low densities than at higher densities.

An Allee effect can arise from a large variety of different ecological mechanisms. There are several types of reproductive Allee effects, as fertilization efficiency in sessile organisms, mate finding in mobile organisms or cooperative breeding. Examples also include mechanisms related to survival, like environmental conditioning and predation. Comprehensive description of the various mechanisms with appropriate ecological examples can be found in Berec et al. (2007), Stephens and Sutherland (1999), Courchamp et al. (2008). Predation can generate a strong Allee effect in prey. An example for this mechanism is the case of the island fox (prey) and the golden eagle (predator) on the California Channel Islands (Angulo et al., 2007). Foxes are consumed by eagles as secondary prey, since feral pigs are the main prey for eagles. If pigs are not present on an island, then eagles will not sustain a permanent population on that habitat, as the fox population by itself cannot provide enough prey. If, on the other hand, there are sufficient pigs around to maintain the eagle population then the eagles establish residence on the island. This way, eagle population dynamics do not depend on fox density, and unlike in the classical predator–prey models, eagles can deplete the fox population without negative feedback on the predator population. If the eagle kill rate follows a Holling type II functional response then this phenomenon reveals an Allee effect in the fox population, since the lower the fox density, the higher the individual risk of eagle predation (Angulo et al., 2007). Clutton-Brock et al. (1999) also compared survival between prey populations living in sites where predators are abundant and sites where predators have been reduced or removed as a result of human interference. They find that suricates in Kalahari Gemsbok Park – an area of high predator density – were subject to a strong Allee effect whilst those living in the neighbouring ranchland where predator density is relatively low, could survive even in small groups.

If the mechanism that triggers the Allee effect depends on ecological circumstances (e.g., presence of particular predators), then the Allee effect may be present in some areas or time periods, and absent in others. Sinclair et al. (1998) investigates the impact of reintroducing endangered predators on the prey. Since predation causes an Allee effect in the prey population which is not the primary food supply for the predator, it might be necessary to apply predator control to allow the escape of the prey population.

In Australia, several indigenous mammals – the black-footed rock wallaby and the quokka for instance – have been reduced to a fraction of their former range, so for their conservation some sensitive prey species are now confined to outer islands where exotic predators (feral cats and red foxes) are absent. Sometimes different habitats support different colony sizes, and it depends on their density whether the population is subject to an Allee effect or grows logistically. Pollock apply two types of strategies for protection from predators. Fish who live in structured habitats (such as algal beds) disperse to reduce detection by predators, so predation triggers a negative density dependence in fish. On the other hand, in open intertidal habitats the fish shoal, which means that their risk-dilution effect is positively density dependent (Stephens and Sutherland, 1999).

The term “metapopulation” was introduced in the works of Levins (1969, 1970), referring to a collection of local populations that are connected by migration (Levins, 1970). The metapopulation concept, though it has undergone some paradigm shift, has been firmly established in population ecology and conservation biology since the work of Hanski and Gilpin (1991), and the topic is also receiving increasing attention in mathematical modelling of ecological processes. The classical metapopulation theory (Levins, 1969) rests on the assumptions that dynamics of local populations occur on a fast time scale in comparison with metapopulation dynamics. This way, the classical metapopulation theory is concerned with the number of local populations but changes in their sizes is ignored. The dynamic theory of island biogeography (MacArthur and Wilson, 1963, 1967), models the changes in the size of local population in the discrete habitat fragments (patches). In a mathematical model that rests on the island theory approach the dynamic variable is the number of individuals on a particular patch, while in the classical approach the dynamic variable is the number of habitat fragments occupied by the species. Hanski (2001) explains how the two metapopulation approaches can be integrated by providing a theoretical framework that explicitly unites the two theories.

In this paper we focus on the approach where the size of local populations is modelled. Most literature with this approach assume negatively density-dependent (typically, logistic) growth in the local populations (Levins, 1969, 1970; Levin, 1974; Holt, 1985; Hastings, 1993; Doebeli, 1995; Allen et al., 1993; Ruxton, 1993, 1994; Poethke and Hovestadt, 2002; Yakubu and Castillo-Chavez, 2002). Besides, spatial theory for the case when the local dynamics is governed by the Allee effect is also relatively well developed (Dennis, 1989; Courchamp et al., 2008; Lewis and Kareiva, 1993; Amarasekare, 1998; Gyllenberg et al., 1999; Keitt et al., 2001; Boukal and Berec, 2002; Kang and Lanchier, 2011). However, an interesting question – that has not been studied yet – is how dispersal and spatial heterogeneity influence metapopulation dynamics when the nature of local density-dependence is negative in some patches but positive in others. Throughout the above discussion we provided examples for real animal metapopulations where in some habitats local populations grow logistically while different locations exhibit an Allee effect. Such difference in the local dynamics can arise when some ecological circumstances (e.g., presence of particular predators) vary over the localities.

We consider an animal population distributed over several discrete geographical patches that are interconnected by dispersal. If a local population is subject to a strong Allee effect then typically it has three steady states: the extinction (zero) equilibrium attracts every solution started below a positive equilibrium (Allee threshold, unstable), and all solutions converge to the population carrying capacity (another positive, stable equilibrium) if the initial population size is larger than the Allee threshold. On the other hand, in a local population that follows logistic growth there exist

only two steady states: the extinction equilibrium is unstable, while the positive steady state – representing population carrying capacity – is globally stable. Studying the dynamics of animal population where density dependence varies over spatial locations has not received much attention despite the numerous examples in real ecosystems (Stephens and Sutherland, 1999; Angulo et al., 2007; Clutton-Brock et al., 1999; Sinclair et al., 1998). Here we show that if some of the patches are subject to a strong Allee effect then many steady states exist. Our accurate mathematical description characterizes the structure and the stability of the equilibria in terms of local density dependence and the migration routes between the patches. Due to the coexistence of many positive stable steady states, making predictions for the future behaviour of such systems can be rather challenging.

## 1. Mathematical model

We consider  $r$  patches, and denote the population of patch  $i$  at time  $t$  by  $N_i(t)$  for  $i = 1, \dots, r$  and  $t \geq 0$ . Population growth at patch  $i$  is modelled by the term  $N_i \cdot g_i(N_i)$  in an ordinary differential equation. This formulation immediately implies that each patch has an extinction state. We assume that  $g_i$  is  $r - 1$  times continuously differentiable for each  $i \in \{1, \dots, r\}$ , and consider two different scenarios for population growth in the patches. We assume that for  $s$  patches ( $0 \leq s \leq r$ ) the population is subject to a strong Allee effect, while the population growth is given by the logistic function for the remaining  $r - s$  patches. To model this, we assume that  $\underline{g}_a$  ( $a \leq s$ ) has two zeros: one gives the unstable Allee threshold  $\bar{A}_a$  (sometimes also called the extinction threshold), and another corresponds to the stable carrying capacity  $\bar{K}_a$ ; and we assume that  $\underline{g}_b$  ( $s + 1 \leq b \leq r$ ) has only one zero, representing the stable carrying capacity  $\bar{K}_b$  of the patch. This is formulated mathematically as

$$\begin{aligned} \frac{d(N_a \cdot \underline{g}_a(N_a))}{dN_a} &= \underline{g}_a(N_a) + N_a \frac{d\underline{g}_a(N_a)}{dN_a} \\ &\begin{cases} < 0 & \text{if } N_a = 0, \\ > 0 & \text{if } N_a = \bar{A}_a, \\ < 0 & \text{if } N_a = \bar{K}_a, \end{cases} \quad \text{for } a \leq s, \\ \frac{d(N_b \cdot \underline{g}_b(N_b))}{dN_b} &= \underline{g}_b(N_b) + N_b \frac{d\underline{g}_b(N_b)}{dN_b} \\ &\begin{cases} > 0 & \text{if } N_b = 0, \\ < 0 & \text{if } N_b = \bar{K}_b, \end{cases} \quad \text{for } s + 1 \leq b \leq r, \end{aligned} \quad (1)$$

where  $0 < \bar{A}_a < \bar{K}_a$  for  $a \leq s$ . Furthermore, we assume that  $\underline{g}_a(0) < 0$  when  $a \leq s$  and  $\underline{g}_b(0) > 0$  when  $s + 1 \leq b \leq r$ , that is, the extinction steady state of a patch is asymptotically stable if a strong Allee effect can occur in the population, and unstable for a patch with logistic population growth. Logistic population growth is typically modelled with  $\underline{g}_b(N_b) = r_b(\bar{K}_b - N_b)$ , and numerous examples for the mathematical formulations of the Allee effect can be found in the literature that satisfy our general assumptions on  $\underline{g}_a$ , e.g.  $\underline{g}_a(N_a) = r_a(\bar{K}_a - N_a)(N_a - \bar{A}_a)$  (Dennis, 1989; Amarasekare, 1998; Asmussen, 1979; Gruntfest et al., 1997; Hopf and Hopf, 1985; Levin and Segel, 1985).

Spatial dispersal between the patches is represented by linear terms in the system for the metapopulation dynamics. We let  $\alpha \cdot c^{ji} N_i$  for the migration term from patch  $i$  to patch  $j$ , where the non-negative constant  $c^{ji}$  ( $i, j \in \{1, \dots, r\}$ ,  $i \neq j$ ) represents connectivity potential, and  $\alpha \geq 0$  is the general dispersal parameter, which will serve as a perturbation parameter as well. The following differential equation system  $(M_\alpha)$  describes population growth

over time in  $r$  locations:

$$\begin{aligned} \frac{d}{dt} N_i &= N_i \cdot g_i(N_i) - \sum_{\substack{j=1 \\ j \neq i}}^r \alpha \cdot c^{ji} N_i \\ &+ \sum_{\substack{j=1 \\ j \neq i}}^r \alpha \cdot c^{ij} N_j, \quad i = 1, \dots, r. \end{aligned} \quad (M_\alpha)$$

Standard results from the theory of differential equations (De Vries et al., 2006) guarantee that the system is well-posed. We denote our model by  $(M_0)$  in the special case when there is no spatial dispersal between the patches, that is,  $\alpha = 0$  and the habitats are isolated.

## 2. Extinction equilibrium and steady states where all local populations are abundant

Equilibria of the model  $(M_\alpha)$  arise as solutions of the steady state system

$$N_i \cdot g_i(N_i) - \sum_{\substack{j=1 \\ j \neq i}}^r \alpha \cdot c^{ji} N_i + \sum_{\substack{j=1 \\ j \neq i}}^r \alpha \cdot c^{ij} N_j = 0, \quad i = 1, \dots, r. \quad (2)$$

One immediately derives the following result, that holds for any  $\alpha$  and  $c^{ij}$  ( $i, j \in \{1, \dots, r\}$ ,  $i \neq j$ ).

**Theorem 2.1.** *The system  $(M_\alpha)$  has a steady state that corresponds to extinction in all habitats.*

In the special case when there is no spatial dispersal between the patches (that is,  $\alpha = 0$ ) the steady state system (2) reads

$$N_i \cdot g_i(N_i) = 0, \quad i = 1, \dots, r,$$

where we see that the equations decouple, and solving the system requires solving  $r$  scalar equations which are pairwise independent. There are  $s$  patches that exhibit a strong Allee effect and each has 3 equilibria, moreover all  $r$  patches with logistic growth have 2 steady states; therefore, there are  $3^s \cdot 2^{r-s}$  equilibria in the system  $(M_0)$  of isolated populations. For a steady state  $\bar{N}^0 = (\bar{N}_1^0, \dots, \bar{N}_r^0)$  of  $(M_0)$  it holds that  $\bar{N}_a^0 \in \{0, \bar{A}_a, \bar{K}_a\}$  for  $a \leq s$  and  $\bar{N}_b^0 \in \{0, \bar{K}_b\}$  for  $s + 1 \leq b \leq r$ .

Whereas finding the solutions is fairly trivial in the case of isolated patches, solving the steady state system (2) can be very difficult and sometimes impossible when dispersal is incorporated. However, by knowing the roots of (2) without dispersal, the implicit function theorem (see Krantz and Parks, 2012 for reference) enables us to retrieve some information on the steady states for small values of dispersal. To this end, we rewrite the system  $(M_\alpha)$  in the compact form

$$\frac{d}{dt} \mathcal{X} = \mathcal{T}(\alpha, \mathcal{X}) \quad (3)$$

with  $\mathcal{X} = (N_1, \dots, N_r)^T \in \mathbb{R}^r$  and  $\mathcal{T} = (\mathcal{T}_1, \dots, \mathcal{T}_r)^T: \mathbb{R} \times \mathbb{R}^r \rightarrow \mathbb{R}^r$ , where  $\mathcal{T}_i$  is defined as the right hand side of the  $i$ th equation of the system  $(M_\alpha)$ ,  $i \in \{1, \dots, r\}$ . Note that (3) is equivalent to  $(M_0)$  in the special case when  $\alpha = 0$ .

The steady state system (2) can be formulated as  $\mathcal{T}(\alpha, \mathcal{X}) = 0$ . When the patches are isolated then this equation reads  $\mathcal{T}(0, \mathcal{X}) = 0$ , and we have a perfect understanding of the roots. To apply the implicit function theorem, we note that  $\mathcal{T}$  is an  $r - 1$  times continuously differentiable function on  $\mathbb{R} \times \mathbb{R}^r$ , and the matrix  $(\frac{\partial \mathcal{T}}{\partial \mathcal{X}})(0, \bar{N}^0)$  is invertible for any equilibrium  $\bar{N}^0$  of the system  $(M_0)$ . Indeed,  $(\frac{\partial \mathcal{T}}{\partial \mathcal{X}})(0, \bar{N}^0)$  is a diagonal matrix with diagonal

elements  $\frac{d}{dN_i}(N_i g_i(N_i))|_{N_i=\bar{N}_i^0}$ ,  $i = 1, \dots, r$ , that are nonzero. The implicit function theorem then says:

Consider an equilibrium  $\bar{N}^0$  of the model  $(M_0)$ . There exists a positive constant  $\alpha_E$ , an open set  $U_E$  containing  $\bar{N}^0$ , and a unique  $r - 1$  times continuously differentiable function  $\bar{N} = (\bar{N}_1, \dots, \bar{N}_r)^T : [0, \alpha_E) \rightarrow U_E$  such that  $\bar{N}(0) = \bar{N}^0$  and  $\mathcal{T}(\alpha, \bar{N}(\alpha)) = 0$  for  $\alpha \in [0, \alpha_E)$ .

We arrive at the following result.

**Theorem 2.2.** Consider an equilibrium  $\bar{N}^0$  of the disconnected system  $(M_0)$ . If  $\alpha$  is sufficiently small then there is a fixed point  $\bar{N}(\alpha)$  of  $(M_\alpha)$ , and this fixed point is close to  $\bar{N}^0$ . In particular, if  $\bar{N}^0$  is a componentwise positive equilibrium of  $(M_0)$  and  $\alpha$  is sufficiently small then the system  $(M_\alpha)$  has a componentwise positive steady state  $\bar{N}(\alpha)$ , which is close to  $\bar{N}^0$ .

We make an important remark on the stability of steady states, that is proved in the Appendix.

**Remark 2.3.** For small values of dispersal local stability of a steady state  $\bar{N}(\alpha)$  of the system  $(M_\alpha)$  is the same as that of the associated equilibrium  $\bar{N}^0$  of the system  $(M_0)$  of isolated local populations. An equilibrium of  $(M_0)$  is stable if all local populations are at stable steady states in the corresponding local dynamics, and the equilibrium is unstable otherwise.

The extinction steady state is stable if all patches exhibit a strong Allee effect, and unstable if there is at least one patch with logistic growth. The system  $(M_0)$  has exactly  $2^s$  componentwise positive equilibria when there are  $s$  patches with Allee dynamics. Therefore, it is guaranteed that there exist at least  $2^s$  positive equilibria in the model  $(M_\alpha)$  (though, only one of these equilibria is stable, see the proof of Remark 2.3 in the Appendix). In the following sections we investigate how dispersal is able to create some additional positive equilibria (many of which are stable).

### 3. Mixed steady states with extinct, rescued or abundant local populations

Other than the extinction steady state and componentwise positive equilibria, the system  $(M_0)$  also has equilibria with mixed zero and positive components. In fact, in  $(M_0)$  there are  $3^s \cdot 2^{r-s} - 1 - 2^s$  such boundary equilibria (which is the total number minus the zero equilibrium minus the ones with all components being positive), that correspond to situations when in the absence of spatial dispersal, some local populations are at positive states while other patches are at zero state. Now we consider such a steady state  $\bar{N}^0$  of the system  $(M_0)$  of isolated local populations. A boundary equilibrium of  $(M_0)$  might disappear when spatial dispersal between the patches is introduced: mathematically speaking, for some  $\alpha > 0$  the unique continuous function  $\bar{N}(\alpha)$  associated with  $\bar{N}^0$  may have negative components. In other words, the boundary equilibrium moves out from the non-negative cone and hence it does not give a biologically meaningful steady state. On the other hand,  $\bar{N}(\alpha) \geq 0$  means that the boundary equilibrium  $\bar{N}^0$  of  $(M_0)$  is preserved for small values of dispersal.

In what follows we describe a mathematical procedure to decide whether a fixed point  $\bar{N}(\alpha)$  associated to a boundary equilibrium of  $(M_0)$ , gives a biologically meaningful steady state in the system  $(M_\alpha)$ . Applying the procedure to each of the  $3^s \cdot 2^{r-s} - 1 - 2^s$  boundary equilibria of  $(M_0)$ , will allow us to give a lower estimate on the number of steady states in  $(M_\alpha)$  (equilibria other than those associated to boundary equilibria of  $(M_0)$ , may also arise with dispersal). We introduce some notation for convenience.

**Definition 3.1.** Consider a boundary equilibrium  $\bar{N}^0$  of the system  $(M_0)$ .

- If a patch  $i$  is extinct in  $\bar{N}^0$  (that is,  $\bar{N}_i^0 = 0$ ), then we say that patch  $i$  is EAD (Extinct in the Absence of spatial Dispersal) in  $\bar{N}^0$ .
- If a patch  $j$  is occupied in  $\bar{N}^0$  (that is,  $\bar{N}_j^0 > 0$ ), then we say that patch  $j$  is OAD (Occupied in the Absence of spatial Dispersal) in  $\bar{N}^0$ .

We note that only those components of  $\bar{N}(\alpha)$  can be negative that correspond to EAD patches, that is, that are zero in  $\bar{N}^0$ . We give a remark to characterize whether a boundary equilibrium remains biologically meaningful when dispersal with small rates is introduced into the system. This result follows from Theorem 2.2.

**Remark 3.2.** Consider a boundary equilibrium  $\bar{N}^0$  of the system  $(M_0)$ .

- If  $\frac{d\bar{N}_i}{d\alpha}(0) > 0$  holds for every EAD patch  $i$  then  $\bar{N}(\alpha)$  is positive if  $\alpha$  is small, that is, for small  $\alpha$  the function  $\bar{N}(\alpha)$  gives a positive steady state in the system  $(M_\alpha)$ .
- If there is an EAD patch  $k$  such that  $\frac{d\bar{N}_k}{d\alpha}(0) < 0$  then  $\bar{N}_k(\alpha)$  is negative for any small  $\alpha$ , which means that the function  $\bar{N}(\alpha)$  does not give a biologically meaningful steady state in the system  $(M_\alpha)$ .

To derive  $\frac{d\bar{N}_i}{d\alpha}(0)$  we differentiate the steady state equation  $\mathcal{T}_i(\alpha, \bar{N}) = 0$ , and then evaluate at  $\alpha = 0$ . Since

$$\begin{aligned} \frac{d}{d\alpha} \left( g_i(\bar{N}_i(\alpha)) \bar{N}_i(\alpha) - \sum_{\substack{j=1 \\ j \neq i}}^r \alpha c^{ji} \bar{N}_j(\alpha) + \sum_{\substack{j=1 \\ j \neq i}}^r \alpha c^{ij} \bar{N}_j(\alpha) \right) \\ = \frac{d}{d\alpha} g_i(\bar{N}_i(\alpha)) \cdot \bar{N}_i(\alpha) + g_i(\bar{N}_i(\alpha)) \frac{d\bar{N}_i}{d\alpha}(\alpha) - \sum_{\substack{j=1 \\ j \neq i}}^r c^{ji} \bar{N}_j(\alpha) \\ - \sum_{\substack{j=1 \\ j \neq i}}^r \alpha c^{ji} \frac{d\bar{N}_i}{d\alpha}(\alpha) + \sum_{\substack{j=1 \\ j \neq i}}^r c^{ij} \bar{N}_j(\alpha) + \sum_{\substack{j=1 \\ j \neq i}}^r \alpha c^{ij} \frac{d\bar{N}_j}{d\alpha}(\alpha) = 0 \end{aligned}$$

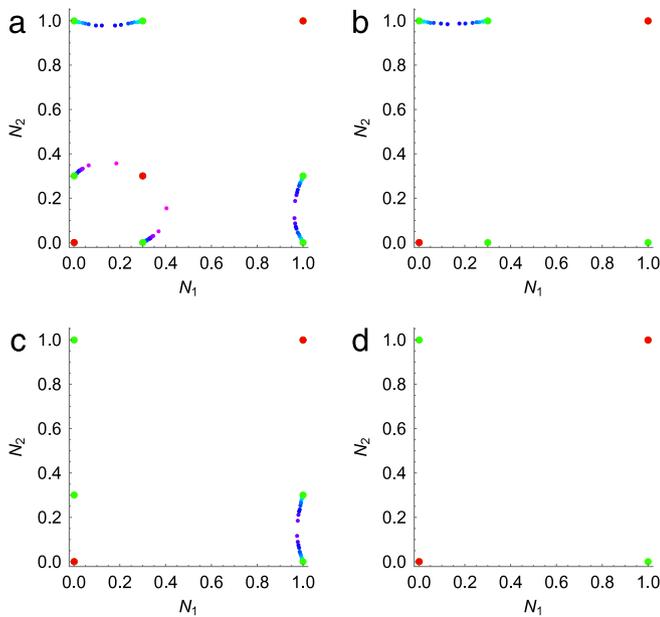
holds whenever  $i$  is an EAD patch, at  $\alpha = 0$  we obtain

$$g_i(0) \frac{d\bar{N}_i}{d\alpha}(0) + \sum_{\substack{j=1 \\ j \neq i}}^r c^{ij} \bar{N}_j^0 = 0,$$

where we used that  $\bar{N}_j(0) = \bar{N}_j^0$  for  $j = 1, \dots, r$ , and  $\bar{N}_i^0 = 0$ . It holds that  $g_i(0) \neq 0$ , so we derive the following equation for the derivative, when  $i$  is an EAD patch:

$$\frac{d\bar{N}_i}{d\alpha}(0) = - \frac{\sum_{\substack{j=1 \\ j \neq i}}^r c^{ij} \bar{N}_j^0}{g_i(0)}. \tag{4}$$

Assume for now that individuals can move directly from any patch to any other habitat, that is,  $c^{ij} > 0$  for all  $i, j \in \{1, \dots, r\}$ . This means that the migration network is fully connected, i.e., it forms a complete graph. Since  $\bar{N}^0$  is a boundary equilibrium, it has some positive components, which implies that  $\sum_{\substack{j=1 \\ j \neq i}}^r c^{ij} \bar{N}_j^0$  is positive. Thus, the sign of the derivative in (4) is opposite of that of  $g_i(0)$ . We recall that  $g_i(0) < 0$  when the population of patch  $i$  is subject to a strong Allee effect, and  $g_i(0) > 0$  for a patch with logistic population growth. Thus, we conclude that the derivative  $\frac{d\bar{N}_i}{d\alpha}(0)$  is positive if a strong Allee effect can occur in patch  $i$ , while it is negative if the population growth is given by the logistic function. Summarizing, we state this result in the form of a theorem. We give Fig. 1 for an illustration of these findings.



**Fig. 1.** Structure of steady states in the model  $(M_\alpha)$  for two patches, when individuals can move from patch 1 to 2, and from patch 2 to 1 (that is, the migration network forms a complete graph). In Figure (a) both patches are subject to a strong Allee effect, (b) patch 1 is subject to a strong Allee effect and growth is logistic in patch 2, (c) growth is logistic in patch 1 and patch 2 is subject to a strong Allee effect, (d) growth is logistic in both patches. Red dots indicate equilibria that exist for all movement rates. Steady states which exist only when the patches are disconnected ( $\alpha = 0$ ) are indicated with green dots. We illustrate by changing the colour from green through blue and violet to red, how these equilibria wander in the positive cone as dispersal parameter increases from 0 to 1. For these simulations, we use  $g_a(N_a) = r_a(\bar{K}_a - N_a)(N_a - \bar{A}_a)$  for Allee patches and  $g_b(N_b) = r_b(\bar{K}_b - N_b)$  for patches with logistic growth,  $r_1 = 1$ ,  $r_2 = 1.3$ ,  $c^{12} = 1$ ,  $c^{21} = 1$ ,  $\bar{K}_1 = 1$ ,  $\bar{K}_2 = 1$ ,  $\bar{A}_1 = 0.3$ ,  $\bar{A}_2 = 0.3$ . (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Theorem 3.3.** Consider a boundary equilibrium  $\bar{N}^0$  of the system  $(M_0)$  for isolated local populations, and assume that individuals can move freely between the patches. If all the EAD habitats (that is, extinct in  $\bar{N}^0$ ) are subject to a strong Allee effect, then for small  $\alpha$  the associated fixed point  $\bar{N}(\alpha)$  of the system  $(M_\alpha)$  gives a positive equilibrium. Otherwise,  $\bar{N}(\alpha)$  has some negative components for any small  $\alpha$ , and thus it does not give a biologically meaningful equilibrium.

Spatial dispersal of populations is influenced by numerous environmental factors, as distance between habitats, fitness of individuals, or human interference that limit accessibility of certain geographic areas. One can think of various reasons why two habitats are not connected, or are connected by a one-way route only. In our mathematical model, such a scenario is implemented by setting one or more connectivity potential parameters to zero. If  $c^{ij} = 0$  holds, then no individual migrates from patch  $j$  to  $i$  directly (however, this does not necessarily mean that  $i$  is unreachable from  $j$  as there may exist an indirect way via other locations). When investigating whether a fixed point  $\bar{N}(\alpha)$  associated to a boundary equilibrium  $\bar{N}^0$  of  $(M_0)$  gives a biologically meaningful steady state in the system  $(M_\alpha)$  with spatial dispersal, we look at the derivative of the function at all patches that are extinct without dispersal (see Remark 3.2). By Eq. (4), such derivatives are non-zero as long as the sum in the numerator of (4) is non-zero, that is,

$$\frac{d\bar{N}_i}{d\alpha}(0) \neq 0 \iff \sum_{\substack{j=1 \\ j \neq i}}^r c^{ij} \bar{N}_j^0 \neq 0.$$

We remind that, speaking of a boundary equilibrium with mixed positive and zero components, there always exists a  $j$  such that

$\bar{N}_j^0$  is positive. Thus, if  $c^{ij} > 0$  for all  $j$  (migration to  $i$  is possible from any other patch directly), or  $\bar{N}_j^0 > 0$  and  $c^{ij} > 0$  hold at the same time, then the derivative of  $\bar{N}_i$  is non-zero, and one can easily decide whether  $\bar{N}_i(\alpha)$  is positive or negative for small  $\alpha$ . On the other hand, it is also possible that  $c^{ij} = 0$  whenever  $\bar{N}_j^0 > 0$ , meaning that there is no direct way to  $i$  from patches that are at positive steady state (occupied) in the absence of dispersal. In such case, Eq. (4) is not sufficient to decide whether the fixed point  $\bar{N}(\alpha)$  associated to the boundary equilibrium  $\bar{N}^0$ , gives a biologically meaningful steady state in the system  $(M_\alpha)$ , since the derivative of  $\bar{N}_i$  is zero.

To overcome this difficulty, one has to look at higher order derivatives and the entire network of connections between patches, instead of just looking at locations that directly connect to EAD patches. We give Theorem 3.4 to show that our earlier result in Theorem 3.3 for the special case of a fully connected migration network can be extended to general migration networks. Theorem 3.4 is applicable to an arbitrary connection network between the patches, hence the proof is much more technical than the one for the fully connected migration network in Theorem 3.3. For this reason, we refer the interested reader to the Appendix for the proof, nevertheless present Fig. 2 for the illustration of the result.

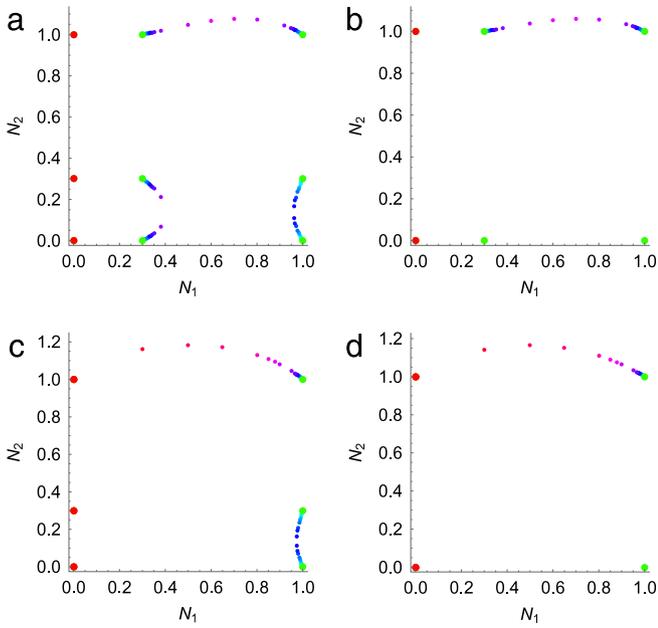
**Theorem 3.4.** Consider a boundary equilibrium  $\bar{N}^0$  of the system  $(M_0)$  for isolated local populations. If there is an EAD patch (that is, extinct in  $\bar{N}^0$ ) with logistic growth, that is reachable (maybe via other patches) from an OAD patch (that is, occupied in  $\bar{N}^0$ ), then for any small  $\alpha$  the associated fixed point  $\bar{N}(\alpha)$  of the system  $(M_\alpha)$  does not give a biologically meaningful equilibrium since  $\bar{N}(\alpha)$  has some negative components. Otherwise,  $\bar{N}(\alpha)$  gives a non-negative equilibrium in the system  $(M_\alpha)$ .

See Fig. 2 for the equilibria in the model  $(M_\alpha)$  in the case when two patches are considered, but patch 1 is not reachable from patch 2. A migration network of five patches is presented in Fig. 3. If local populations are isolated then the system has  $3^2 \cdot 2^3 = 72$  equilibria, 4 of those are stable and the other 68 are unstable. Following the method described in Theorems 2.1, 2.2 and 3.4, one can derive that there are 72 fixed points in the system with small migration values, each associated to an equilibrium of isolated local populations; however, 59 of these fixed points do not give biologically meaningful equilibria, and the system of five patches has 4 stable and 9 unstable steady states for small values of dispersal. In the caption of Fig. 3 we show through two examples how to apply the procedure described in Theorem 3.4.

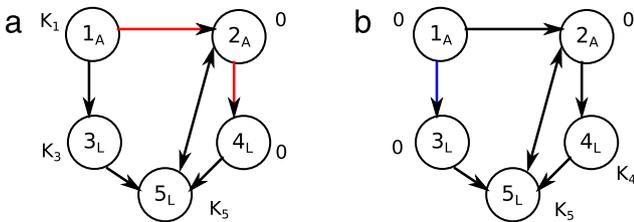
Summarizing, our method exactly determines in a straightforward way whether a boundary steady state of the isolated populations moves out from or moves into the positive cone, when dispersal is introduced. Equilibria moving outwards are ceased to exist as biologically feasible steady states, while equilibria moving inwards persist. The procedure also tells which of those equilibria are stable, and it works for any number of patches and any migration network.

#### 4. Discussion

We illustrated that populations in a patchy environment can have a large number of steady states if a strong Allee effect can occur in some of the habitats. We gave a general mathematical model for the dynamics of a single species when individuals migrate between  $r$  patches that can exhibit two types of local density dependence. Logistic growth and a strong Allee effect are typical examples for negative and positive density dependence, respectively; however, due to the general formulation of the local



**Fig. 2.** Structure of steady states in the model  $(M_\alpha)$  for two patches, when individuals can move from patch 1 to 2, but they cannot from patch 2 to 1. In Figure (a) both patches are subject to a strong Allee effect, (b) patch 1 is subject to a strong Allee effect and growth is logistic in patch 2, (c) growth is logistic in patch 1 and patch 2 is subject to a strong Allee effect, (d) growth is logistic in both patches. Red dots indicate equilibria that exist for all movement rates. Steady states which exist only when the patches are disconnected ( $\alpha = 0$ ) are indicated with green dots. We illustrate by changing the colour from green through blue and violet to red, how these equilibria wander in the positive cone as dispersal parameter increases from 0 to 1. For these simulations, we use  $g_a(N_a) = r_a(K_a - N_a)(N_a - \bar{A}_a)$  for Allee patches and  $g_b(N_b) = r_b(K_b - N_b)$  for patches with logistic growth,  $r_1 = 1, r_2 = 1.3, c^{12} = 0, c^{21} = 1, \bar{K}_1 = 1, \bar{K}_2 = 1, \bar{A}_1 = 0.3, \bar{A}_2 = 0.3$ . (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)



**Fig. 3.** Migration network of five patches, where patches 1 and 2 exhibit a strong Allee effect, and patches 3, 4, and 5 follow logistic growth. The migration pathways are indicated by arrows. In the absence of dispersal, such network of patches has 4 stable and 68 unstable steady states, but only 4 stable and 9 unstable equilibria are biologically meaningful when migration is introduced. Figure (a): Consider the equilibrium  $\bar{N}^0 = (K_1, 0, K_3, 0, K_5)$  of the system of isolated local populations. Then, the associated fixed point  $\bar{N}(\alpha)$  of the system with dispersal will NOT be a biologically meaningful equilibrium: patch 4 is with logistic growth, extinct in the absence of dispersal, and reachable (though, not directly) from patch 1, that is at positive steady state without dispersal. Figure (b): On the other hand, for the equilibrium  $\bar{N}^0 = (0, 0, 0, K_4, K_5)$  of isolated local populations, the associated fixed point  $\bar{N}(\alpha)$  gives a biologically meaningful steady state in the system with dispersal: considering the three patches that follow logistic growth, patches 4 and 5 are at positive states without dispersal, and though patch 3 is extinct when the locations are isolated, it is not reachable from another patch that is at positive state.

growth function  $N_i \cdot g_i(N_i)$ , our model is applicable to a broad range of scenarios for local growth.

After understanding the dynamics of local populations, it is easy to describe all the steady states and their stability when the locations are isolated. If  $s$  patches exhibit a strong Allee effect (having 3 equilibria each) and  $r - s$  patches follow logistic growth (having 2 equilibria each), then the system of disconnected patches has a total number of  $3^s \cdot 2^{r-s}$  equilibria, because from each

patch we can choose one possibility independently. An equilibrium is stable if each component is stable in the corresponding local dynamics, and the equilibrium is unstable otherwise. Thus, there are  $2^s$  stable steady states in the combined population of isolated local populations. On the other hand, finding the steady states in the system with dispersal is difficult. In this paper, we provided a procedure that describes the structure and stability of the steady states for small values of migration between the patches. If the migration network is fully connected, then we found that there are  $3^r$  steady states if all patches exhibit a strong Allee effect ( $s = r$ ), and there exist  $3^s + 1$  equilibria if there is at least one habitat where growth is logistic ( $s < r$ ). Thus, there exists a large number of steady states and this number grows exponentially in the number of locations. But more importantly, the same statement holds for the number of stable equilibria: for fully connected locations there exist  $2^s$  ( $s \leq r$ ) stable steady states when dispersal rates are low. Calculating these numbers for a general migration network (that is, when some patches do not directly connect) is more challenging, and requires the application of the procedure described in [Theorems 2.1, 2.2 and 3.4](#). These results rest on the idea of finding steady states in the system for low dispersal rates by using our knowledge on the steady states of the system without dispersal. More precisely, the procedure identifies equilibria of the system with dispersal that are close to an equilibrium of the system of isolated locations.

When dispersal between the locations is weak, our results hold true for a broad range of parametrization on the local growth. However, such general formulation of the model makes it impossible to extend the steady state analysis to cases when migration rates are higher; depending on the particular form of the local nonlinear growth functions  $N_i \cdot g_i(N_i)$ , a rich variety of dynamics can occur in the model. We illustrated for some specific functional forms in [Figs. 1 and 2](#) how the structure of equilibria changes when dispersal rates vary more widely. We can numerically observe that by increasing the dispersal rate, equilibria collide and disappear in various bifurcations, and generally the situation simplifies when migration is larger. One possible intuitive interpretation is that large dispersal weakens the effect of heterogeneity. The exact behaviour depends on the particular nonlinearities that describe the population growth.

[Amarasekare \(1998\)](#) studied the interaction between local dynamics and dispersal on population persistence in a two-patch model. She found that two local populations that grow logistically are unlikely to go extinct even when rare. Our results for multiple patches with logistic growth agree with those in [Amarasekare \(1998\)](#). We showed that the only stable equilibrium is the one with all local populations at their carrying capacities, whereas all other steady states (if any) are unstable, implying that rare populations are likely to increase. When patches are isolated and all follow Allee dynamics, then the population goes extinct when rare because rare local populations go to their stable extinction states. [Amarasekare \(1998\)](#) showed that dispersal leads to a qualitative change in the two-patch system, that is, a patch below the Allee threshold is rescued from extinction by immigrants from another patch that is above the Allee threshold. Our findings for multiple patches are in accordance with this result, in fact, we can say much more. If all local populations exhibit a strong Allee effect then we showed that there are numerous equilibria including a large number of stable steady states. In particular, if a patch is at the extinction steady state in the isolated system, then immigration from another patch that is at positive state, pushes the extinction state to some positive value, thereby the extinct patch becomes occupied. More importantly, the extinction state of a patch with Allee growth is stable in the local dynamics, which means that weak dispersal creates stable positive equilibria that do not exist without dispersal, and this way local populations will not go

extinct even if near the extinction state. Our results generalize those by Amarasekare since we consider animal populations where growth can vary over the locations.

Regardless of the way local populations grow, the total population of isolated localities has a single componentwise positive stable equilibrium, that corresponds to the patch-wise carrying capacities. In this paper, we showed that a large number of alternate positive stable steady states can exist if some of the patches exhibit a strong Allee effect. From the dynamical systems perspective, such rich structure of stable steady states goes hand in hand with complicated behaviour of the model, that makes predicting the population dynamics particularly difficult.

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**Appendix**

The Appendix is organized as follows. Firstly, Remark 2.3 will be proved. Then, we present several definitions, lemmas, and theorems for the proof of Theorem 3.4.

Remark 2.3 cares for the local stability of equilibria of the system  $(M_\alpha)$ . To this end, we investigate the eigenvalues of the Jacobian of the system (2) evaluated at the equilibria. If all eigenvalues of the Jacobian have negative real parts then the equilibrium is locally asymptotically stable whereas it is unstable if there is an eigenvalue with positive real part. If local populations are isolated (that is,  $\alpha = 0$ ) then the equations of (2) decouple, and the Jacobian is a diagonal matrix with diagonal elements  $\frac{d}{dN_i}(N_i \cdot g_i(N_i))$ ,  $i = 1, \dots, r$ . Thus, eigenvalues arise as the elements in the diagonal, and the stability of an equilibrium  $\bar{N}^0$  of the system  $(M_0)$  for isolated local populations is determined by the sign of  $\frac{d}{dN_i}(N_i \cdot g_i(N_i))|_{N_i=\bar{N}_i^0}$ ,  $i = 1, \dots, r$ . In particular,  $\bar{N}^0$  is locally asymptotically stable if  $\frac{d}{dN_i}(N_i \cdot g_i(N_i))|_{N_i=\bar{N}_i^0} < 0$  holds for  $i = 1, \dots, r$ , and unstable if there is a  $j$  such that  $\frac{d}{dN_j}(N_j \cdot g_j(N_j))|_{N_j=\bar{N}_j^0} > 0$ . In (1) and the discussion afterwards we described the steady states of local populations as well as the stability of these steady states. Note that in the local dynamics, a negative derivative corresponds to stability whereas a positive derivative means instability.

In particular, the extinction equilibrium of the system  $(M_\alpha)$  is stable if all patches exhibit a strong Allee effect ( $s = r$ ), and unstable otherwise. An equilibrium  $\bar{N}^0$  where all patches are occupied, is stable if all local populations are at the carrying capacities (that is,  $\bar{N}_a^0 = \bar{K}_a^0$  and  $\bar{N}_b^0 = \bar{K}_b^0$  for all  $a \leq s$  and  $b \geq s + 1$ ), and unstable otherwise (that is, if there is an  $a$  such that  $\bar{N}_a^0 = \bar{A}_a^0$ ). An equilibrium  $\bar{N}^0$  with some local populations at the extinction state and others abundant, is stable if all patches with logistic growth are at their carrying capacities and patches that are subject to a strong Allee effect, are either extinct or at their carrying capacities (that is,  $\bar{N}_a^0 = 0$  or  $\bar{N}_a^0 = \bar{K}_a^0$  for all  $a \leq s$ , and  $\bar{N}_b^0 = \bar{K}_b^0$  for all  $b \geq s + 1$ ).

We showed that the steady state system (2) can be obtained in the compact form  $\mathcal{T}(\alpha, \mathcal{X}) = 0$ , where  $\alpha$  is the general dispersal parameter and  $\alpha = 0$  means isolated local populations. The Jacobian  $\frac{d\mathcal{T}}{d\mathcal{X}}(\alpha, \mathcal{X})$  is continuous in  $\alpha$  and so is the function  $\bar{N}(\alpha)$ , representing an equilibrium of the system  $(M_\alpha)$  on the interval

$[\alpha, \alpha_E]$  for small  $\alpha_E$ . We remind that the system (2) is equivalent to the system  $(M_0)$  when  $\alpha = 0$ , so by continuity of eigenvalues with respect to parameters, we arrive to the statement of Remark 2.3.

For the proof of Theorem 3.4, we make the following preparation.

**Lemma A.1.** For any positive integer  $n$  such that  $n \leq r - 1$ , it holds that

$$\frac{d^n \bar{N}_i}{d\alpha^n}(\alpha) = - \frac{n \sum_{\substack{j=1 \\ j \neq i}}^r c^{ij} \frac{d^{n-1} \bar{N}_j}{d\alpha^{n-1}}(\alpha)}{g_i(\alpha)}$$

whenever patch  $i$  ( $i \in \{1, \dots, r\}$ ) is EAD in the boundary equilibrium  $\bar{N}^0$ , and  $\frac{d^l \bar{N}_i}{d\alpha^l}(\alpha) = 0$  for every  $l < n$ .

**Proof.** Indeed, we obtain the  $n$ th derivative of the steady state equation  $\mathcal{T}_i(\alpha, \mathcal{X}) = 0$  as

$$\begin{aligned} & \frac{d^n}{d\alpha^n} \left( g_i(\bar{N}_i(\alpha)) \bar{N}_i(\alpha) - \sum_{\substack{j=1 \\ j \neq i}}^r \alpha c^{ji} \bar{N}_i(\alpha) + \sum_{\substack{j=1 \\ j \neq i}}^r \alpha c^{ij} \bar{N}_j(\alpha) \right) \\ &= \sum_{l=0}^n \binom{n}{l} \frac{d^{n-l}}{d\alpha^{n-l}} g_i(\bar{N}_i(\alpha)) \cdot \frac{d^l \bar{N}_i}{d\alpha^l}(\alpha) \\ & \quad - \sum_{l=0}^n \binom{n}{l} \sum_{\substack{j=1 \\ j \neq i}}^r \frac{d^{n-l}(\alpha c^{ji})}{d\alpha^{n-l}} \cdot \frac{d^l \bar{N}_i}{d\alpha^l}(\alpha) \\ & \quad + \sum_{l=0}^n \binom{n}{l} \sum_{\substack{j=1 \\ j \neq i}}^r \frac{d^{n-l}(\alpha c^{ij})}{d\alpha^{n-l}} \cdot \frac{d^l \bar{N}_j}{d\alpha^l}(\alpha) = 0. \end{aligned} \tag{5}$$

Here we used the assumption that  $g_i$  is  $r - 1$  times continuously differentiable. Clearly  $\frac{d^{n-l}(\alpha c^{ij})}{d\alpha^{n-l}} = 0$  whenever  $n - l \geq 2$ , moreover  $\frac{d(\alpha c^{ij})}{d\alpha} = c^{ij}$ , so if  $\frac{d^l \bar{N}_i}{d\alpha^l}(\alpha) = 0$  holds for all  $l < n$  then (5) at  $\alpha = 0$  reads

$$g_i(\bar{N}_i(0)) \frac{d^n \bar{N}_i}{d\alpha^n}(\alpha) + n \sum_{\substack{j=1 \\ j \neq i}}^r c^{ij} \frac{d^{n-1} \bar{N}_j}{d\alpha^{n-1}}(\alpha) = 0. \tag{6}$$

It holds by assumption that  $\bar{N}_i(0) = 0$ , which completes the proof.  $\square$

**Definition A.2.** Consider a patch  $i$  that is EAD in the boundary equilibrium  $\bar{N}^0$ . We define  $D_i$  as the least nonnegative integer such that in the migration network, there is a path that starts with an OAD patch  $j$ , ends with patch  $i$ , and contains  $D_i$  patches in-between. If there is no such path then let  $D_i = r - 1$ .

**Definition A.3.** We characterize connectivity between patches.

- We say that there is a direct connection from patch  $j$  to patch  $i$  if  $c^{ij} > 0$ . We note that if  $i$  is an EAD patch with direct connection from an OAD patch  $j$  then  $D_i = 0$ .
- We say that patch  $i$  is reachable from patch  $j$  if there is a path from  $j$  to  $i$ . We also note that if  $i$  is an EAD patch and there exists a path to  $i$  from an OAD patch then  $D_i \leq r - 2$  holds.

**Lemma A.4.** If  $i$  is an EAD patch in  $\bar{N}^0$ , then it holds that  $\frac{d^l \bar{N}_i}{d\alpha^l}(\alpha) = 0$  whenever  $l \leq D_i$ .

**Proof.** Indeed, the inequality  $D_{i_0} \geq 0$  is satisfied for every patch  $i_0$  with  $\bar{N}_{i_0} = 0$ . The case when  $D_{i_0} = 0$  is trivial, so we consider a patch  $i_1$  for which  $D_{i_1} \geq 1$ , and from Lemma A.1 we derive

$$\frac{d\bar{N}_{i_1}}{d\alpha}(0) = -\frac{\sum_{\substack{j=1 \\ j \neq i_1}}^r c^{i_1 j} \bar{N}_j(0)}{g_{i_1}(0)}.$$

For every  $j$  such that  $c^{i_1 j} \neq 0$ , it follows from  $D_{i_1} \neq 0$  that  $\bar{N}_j(0) = 0$ , thus the right hand side is zero. We obtain that  $\frac{d\bar{N}_{i_1}}{d\alpha}(0) = 0$ .

Next, consider a patch  $i_2$  where  $\bar{N}_{i_2} = 0$  and  $D_{i_2} \geq 2$ . We have  $\frac{d\bar{N}_{i_2}}{d\alpha}(0) = 0$  since  $D_{i_2} \geq 2 \geq 1$ , so Lemma A.1 yields the equation

$$\frac{d^2\bar{N}_{i_2}}{d\alpha^2}(0) = -\frac{2 \sum_{\substack{j=1 \\ j \neq i_2}}^r c^{i_2 j} \frac{d\bar{N}_j}{d\alpha}(0)}{g_{i_2}(0)}.$$

We note that each patch  $j$  for which  $c^{i_2 j} \neq 0$  is EAD since  $D_{i_2} \geq 1$ . Thus, for  $D_j$  it follows that  $D_j \geq 1$ , henceforth  $\frac{d\bar{N}_j}{d\alpha}(0) = 0$  holds by induction, and the right hand side of the last equation is zero. We conclude that  $\frac{d^2\bar{N}_{i_2}}{d\alpha^2}(0) = 0$  holds for all patches where  $D_{i_2} \geq 2$ .

The continuation of this procedure yields that  $\frac{d^l\bar{N}_{i_l}}{d\alpha^l}(0) = 0$  for any patch  $i_l$  where  $D_{i_l} \geq l$  holds. This proves the lemma.  $\square$

**Theorem A.5.** Assume that in the boundary equilibrium  $\bar{N}^0$ , there is a patch  $i$  that is EAD and growth is logistic, furthermore  $i$  is reachable from an OAD patch. Then there is an  $\alpha^* > 0$  such that  $\bar{N}^i(\alpha) < 0$  for  $\alpha \in (0, \alpha^*)$ , which implies that  $\bar{N}(\alpha)$  has a negative component and it does not give a biologically meaningful equilibrium in  $(M_\alpha)$ .

**Proof.** The proof is by contradiction. Assume that  $\bar{N}^0$  is such that there are patches  $i_0$  and  $i_+$  such that  $\bar{N}_{i_0} = 0, \bar{N}_{i_+} > 0$ , in  $i_0$  the population growth is logistic,  $i_0$  is reachable from  $i_+$ , and there exists an  $\alpha^{**} > 0$  such that  $\bar{N}(\alpha) \geq 0$  on  $[0, \alpha^{**}]$ . If patches  $i_0$  and  $i_+$  – as described above – exist then there is a minimal distance between such patches, i.e., there exists a least nonnegative integer  $L \leq r - 2$  such that there is a path from an OAD patch via  $L$  patches to a patch which is EAD in  $\bar{N}_0$  and with logistic growth. We denote by  $i$  this patch in the shortest path, and let  $i_{L+1}^*$  be the OAD patch.

In the case when  $L = 0$ , Lemma A.1 immediately yields contradiction. Indeed, as  $c^{i, i_{L+1}^*} > 0, \bar{N}_{i_{L+1}^*} > 0$ , and  $g_i(0) > 0$  (the population growth is logistic in  $i$ ), the equation

$$\frac{d\bar{N}_i}{d\alpha}(0) = -\frac{\sum_{\substack{j=1 \\ j \neq i}}^r c^{ij} \bar{N}_j(0)}{g_i(0)}$$

yields  $\frac{d\bar{N}_i}{d\alpha}(0) < 0$ . Next, we assume that  $L \geq 1$ . We label the patches in the minimal-length path by  $i, i_1^*, \dots, i_L^*, i_{L+1}^*$ . We note that  $\bar{N}_i^0 = \bar{N}_{i_1^*}^0 = \dots, \bar{N}_{i_L^*}^0 = 0, \bar{N}_{i_{L+1}^*}^0 > 0$ , moreover by the minimality of  $L$  the patches  $i_1^*, \dots, i_L^*$  cannot follow logistic growth. Instead, there is a strong Allee effect in patch  $i_j^*$  for  $j = 1, \dots, L$ , and hence  $g_{i_j^*}(0) < 0$  holds.

By Lemma A.1,  $\bar{N}_{i_L^*}^0 = 0$  yields

$$\frac{d\bar{N}_{i_L^*}}{d\alpha}(0) = -\frac{\sum_{\substack{j=1 \\ j \neq i_L^*}}^r c^{i_L^* j} \bar{N}_j(0)}{g_{i_L^*}(0)}.$$

The equation has a positive right hand side since  $\bar{N}_{i_{L+1}^*}^0 = \bar{N}_{i_{L+1}^*}^*(0) > 0$  and  $g_{i_L^*}(0) < 0$ , which implies that  $\frac{d\bar{N}_{i_L^*}}{d\alpha}(0) > 0$ . A similar equation

$$\frac{d\bar{N}_{i_{L-1}^*}}{d\alpha}(0) = -\frac{\sum_{\substack{j=1 \\ j \neq i_{L-1}^*}}^r c^{i_{L-1}^* j} \bar{N}_j(0)}{g_{i_{L-1}^*}(0)}$$

follows from  $\bar{N}_{i_{L-1}^*}^0 = 0$  and Lemma A.1. We note that  $D_{i_{L-1}^*} = 1$ , hence  $\bar{N}_j(0) = 0$  holds for every  $j$  such that  $c^{i_{L-1}^* j} \neq 0$ . The zero numerator yields  $\frac{d\bar{N}_{i_{L-1}^*}}{d\alpha}(0) = 0$ , so we can apply Lemma A.1 to derive

$$\frac{d^2\bar{N}_{i_{L-1}^*}}{d\alpha^2}(0) = -\frac{2 \sum_{\substack{j=1 \\ j \neq i_{L-1}^*}}^r c^{i_{L-1}^* j} \frac{d\bar{N}_j}{d\alpha}(0)}{g_{i_{L-1}^*}(0)}.$$

If there is a  $j$  such that  $c^{i_{L-1}^* j} \neq 0$  and  $\frac{d\bar{N}_j}{d\alpha}(0) < 0$ , then  $\bar{N}_j(\alpha)$  is negative for small  $\alpha$  and hence  $\bar{N}(\alpha)$  is not in the nonnegative cone, which violates our assumption that  $\bar{N}(\alpha) \geq 0$  for  $\alpha$  sufficiently small. Thus, each such derivative is necessarily nonnegative, moreover we have showed that  $\frac{d\bar{N}_{i_{L-1}^*}}{d\alpha}(0) > 0$  is satisfied, which makes the numerator positive. This implies  $\frac{d^2\bar{N}_{i_{L-1}^*}}{d\alpha^2}(0) > 0$  since  $g_{i_{L-1}^*}(0) < 0$ .

Next, we consider patch  $i_{L-2}^*$ , where  $D_{i_{L-2}^*} = 2$ . For any patch  $j$  for which  $c^{i_{L-2}^* j} \neq 0$ , it holds that  $D_j \geq 1$ , thus  $\bar{N}_j(0) = 0$  and  $\frac{d\bar{N}_j}{d\alpha}(0) = 0$  hold by Lemma A.4. Thus, the right hand side of equation

$$\frac{d\bar{N}_{i_{L-2}^*}}{d\alpha}(0) = -\frac{\sum_{\substack{j=1 \\ j \neq i_{L-2}^*}}^r c^{i_{L-2}^* j} \bar{N}_j(0)}{g_{i_{L-2}^*}(0)}$$

is zero, so it follows that  $\frac{d\bar{N}_{i_{L-2}^*}}{d\alpha}(0) = 0$ , and thus Lemma A.1 yields

$$\frac{d^2\bar{N}_{i_{L-2}^*}}{d\alpha^2}(0) = -\frac{2 \sum_{\substack{j=1 \\ j \neq i_{L-2}^*}}^r c^{i_{L-2}^* j} \frac{d\bar{N}_j}{d\alpha}(0)}{g_{i_{L-2}^*}(0)}.$$

We obtain again that  $\frac{d^2\bar{N}_{i_{L-2}^*}}{d\alpha^2}(0) = 0$  since all derivatives in the right hand side are zero. Finally, by Lemma A.1 we derive

$$\frac{d^3\bar{N}_{i_{L-2}^*}}{d\alpha^3}(0) = -\frac{3 \sum_{\substack{j=1 \\ j \neq i_{L-2}^*}}^r c^{i_{L-2}^* j} \frac{d^2\bar{N}_j}{d\alpha^2}(0)}{g_{i_{L-2}^*}(0)}.$$

If there is a  $j$  such that  $c^{i_{L-2}^* j} \neq 0$  and  $\frac{d^2\bar{N}_j}{d\alpha^2}(0)$  is negative then so is  $\bar{N}(\alpha)$  for small  $\alpha$  since  $\frac{d\bar{N}_j}{d\alpha}(0) = 0$  and  $\bar{N}_j(0) = 0$ , which is a contradiction. Otherwise, the right hand side of the last equation is positive (it holds that  $c^{i_{L-2}^*, i_{L-1}^*} \neq 0$  and  $\frac{d^2\bar{N}_{i_{L-1}^*}}{d\alpha^2}(0) > 0$ ), thus the positivity of  $\frac{d^3\bar{N}_{i_{L-2}^*}}{d\alpha^3}(0)$  follows from  $g_{i_{L-2}^*}(0) < 0$ .

Following these arguments, one can prove that  $\frac{d^{m+1}\bar{N}_{i_1}^*}{d\alpha^{m+1}}(0) > 0$  for  $m = 0, 1, \dots, L-1$  (we remark that for  $m = L-1$  this reads  $\frac{d^L\bar{N}_{i_1}^*}{d\alpha^L}(0) > 0$ ), and that for any fixed  $m$  and  $k \leq m$ , it holds that  $\frac{d^k\bar{N}_{i_1}^*}{d\alpha^k}(0) = 0$ . We note that  $D_i = L$ , which also means by Lemma A.4 that  $\frac{d^m\bar{N}_i}{d\alpha^m}(0) = 0$  for  $m \leq D_i = L$ . Henceforth, we can apply Lemma A.1 and derive

$$\frac{d^{L+1}\bar{N}_i}{d\alpha^{L+1}}(0) = -\frac{L \sum_{\substack{j=1 \\ j \neq i}}^r c^{i,j} \frac{d^L\bar{N}_j}{d\alpha^L}(0)}{g_i(0)}.$$

$D_i = L$  implies  $D_j \geq L-1$  for any  $j$  for which  $c^{i,j} \neq 0$ , hence  $\frac{d^m\bar{N}_j}{d\alpha^m}(0) = 0$  is satisfied for  $m = 0, 1, \dots, L-1$ . The assumption that  $\bar{N}(\alpha) \geq 0$  for small  $\alpha$  yields that  $\frac{d^L\bar{N}_j}{d\alpha^L}(0) < 0$  is impossible; this, together with  $\frac{d^L\bar{N}_{i_1}^*}{d\alpha^L}(0) > 0$  and  $c^{i,i_1} > 0$ , implies the positivity of the numerator. As  $g_i(0) > 0$  holds, it follows that  $\frac{d^{L+1}\bar{N}_i}{d\alpha^{L+1}}(0)$  is negative, but we showed that  $\frac{d^m\bar{N}_i}{d\alpha^m}(0) = 0$  when  $0 \leq m \leq L$ , so it follows that  $\bar{N}_i(\alpha) < 0$  for small  $\alpha$ , a contradiction. The proof is complete.  $\square$

**Theorem A.6.** Assume that in the boundary equilibrium  $\bar{N}^0$ , there is a strong Allee effect in every EAD patch  $j$  where  $D_j < r-1$ . Then for an EAD patch  $i$  that is subject to a strong Allee effect, it holds that  $\frac{d^{D_i+1}\bar{N}_i}{d\alpha^{D_i+1}}(0) > 0$  if  $D_i < r-1$ , and  $\bar{N}(\alpha) = 0$  if  $D_i = r-1$ .

**Proof.** If  $i$  is at the extinction steady state for  $\alpha = 0$ , and the patch is not reachable from any patch  $j$  with  $\bar{N}_j > 0$  (that is,  $D_i = r-1$ ), then no individuals migrate into  $i$  when spatial dispersal is incorporated, and hence we have  $\bar{N}_i(\alpha) = 0$  for any  $\alpha > 0$ . In the case when  $D_i < r-1$ , the proof is by induction. If  $D_{i_0} = 0$  for a patch  $i_0$  that is subject to a strong Allee effect ( $g_{i_0}(0) < 0$ ) and  $\bar{N}_{i_0}^0 = 0$ , then there is a  $j$  such that  $c^{i_0,j} \neq 0$  and  $\bar{N}_j^0 > 0$ , so

$$\frac{d\bar{N}_{i_0}}{d\alpha}(0) = -\frac{\sum_{\substack{j=1 \\ j \neq i_0}}^r c^{i_0,j} \bar{N}_j(0)}{g_{i_0}(0)}$$

yields  $\frac{d\bar{N}_{i_0}}{d\alpha}(0) > 0$ .

Whenever  $D_{i_1} = 1$  is satisfied in a patch  $i_1$  where  $\bar{N}_{i_1}^0 = 0$  and subject to a strong Allee effect, Lemma A.4 implies  $\frac{d\bar{N}_{i_1}}{d\alpha}(0) = 0$ , so by Lemma A.1 we derive

$$\frac{d^2\bar{N}_{i_1}}{d\alpha^2}(0) = -\frac{2 \sum_{\substack{j=1 \\ j \neq i_1}}^r c^{i_1,j} \frac{d\bar{N}_j}{d\alpha}(0)}{g_{i_1}(0)}.$$

For every  $j$  with  $c^{i_1,j} \neq 0$  and  $1 \leq D_j \leq r-1$ , Lemma A.4 gives  $\frac{d\bar{N}_j}{d\alpha}(0) = 0$ . If there is a  $j$  such that  $D_j = 0$ ,  $j$  is EAD and  $c^{i_1,j} \neq 0$ , then there necessarily is a strong Allee effect in  $j$ , so  $\frac{d\bar{N}_j}{d\alpha}(0) > 0$  holds by induction. Nevertheless, the positivity of the right hand side of the last equation is guaranteed because we know from  $D_{i_1} = 1$  that there must exist a  $j$  where  $D_j = 0$  and  $c^{i_1,j} \neq 0$ , hence the inequality  $\frac{d^2\bar{N}_{i_1}}{d\alpha^2}(0) > 0$  follows.

We assume that the statement of the theorem holds for any EAD patch  $i$  that is subject to a strong Allee effect and  $D_i \leq L$ ,  $0 < L <$

$r-2$ . We consider an EAD patch  $i_{L+1}$  where  $D_{i_{L+1}} = L+1$  and there is to a strong Allee effect, and obtain the equation

$$\frac{d^{L+2}\bar{N}_{i_{L+1}}}{d\alpha^{L+2}}(0) = -\frac{(L+1) \sum_{\substack{j=1 \\ j \neq i_{L+1}}}^r c^{i_{L+1},j} \frac{d^{L+1}\bar{N}_j}{d\alpha^{L+1}}(0)}{g_{i_{L+1}}(0)}$$

by Lemmas A.1 and A.4.  $D_{i_{L+1}} = L+1$  makes  $D_j \geq L$  for each  $j$  where  $c^{i_{L+1},j} \neq 0$ , and from Lemma A.4 we have  $\frac{d^{L+1}\bar{N}_j}{d\alpha^{L+1}}(0) = 0$  for each  $j$  where  $c^{i_{L+1},j} \neq 0$  and  $D_j \geq L+1$ . The case when  $D_j = L$  is only possible if  $j$  is EAD and subject to a strong Allee effect, and for each such  $j$  the inequality  $\frac{d^{L+1}\bar{N}_j}{d\alpha^{L+1}}(0) > 0$  holds by induction. There exists a  $j$  such that  $c^{i_{L+1},j} > 0$  and  $D_j = L$ , hence the right hand side of the last equation is positive. We derive that  $\frac{d^{L+2}\bar{N}_{i_{L+1}}}{d\alpha^{L+2}}(0) > 0$ , which completes the proof.  $\square$

**Theorem A.5** ensures that for a boundary equilibrium  $\bar{N}(0) = \bar{N}^0$  of  $(M_0)$ , the point  $\bar{N}(\alpha)$  will not be a biologically meaningful fixed point of the system  $(M_\alpha)$  if there is a EAD patch  $i$  in  $\bar{N}^0$  where population growth is logistic and  $i$  is reachable from an OAD patch. On the other hand, a boundary equilibrium  $\bar{N}(0) = \bar{N}^0$  of  $(M_0)$  will persist for small values of spatial dispersal if in all EAD patches of  $\bar{N}^0$  that are reachable from an OAD patch, a strong Allee effect can occur. More precisely, in Theorem A.6 we show that  $\bar{N}_i$  has a positive derivative whenever patch  $i$  is EAD, subject to a strong Allee effect, and reachable from an OAD patch  $j$ . Then, by Lemma A.4, the statement yields that  $\bar{N}_i(\alpha)$  is positive for small  $\alpha$ . EAD patches that are unreachable from OAD patches will not become occupied with the introduction of spatial dispersal. This last remark, together with Theorems A.5 and A.6, proves Theorem 3.4.

## References

- Allee, W.-C., 1931. *Animal Aggregations, A Study in General Sociology*. University of Chicago Press, Chicago.
- Allee, W.-C., Bowen, E., 1932. Studies in animal aggregations: mass protection against colloidal silver among goldfishes. *J. Exp. Zool.* 61, 185–207.
- Allen, J.-C., Schaffer, W.-M., Rosko, D., 1993. Chaos reduces species extinctions by amplifying local population noise. *Nature* 364, 229–232.
- Amarasekare, P., 1998. Interactions between local dynamics and dispersal: Insights from single species models. *Theor. Popul. Biol.* 53, 44–59.
- Angulo, E., Roemer, G.-W., Berec, L., Gascoigne, J., Courchamp, F., 2007. Double Allee effects and extinction in the island fox. *Conserv. Biol.* 21 (4), 1082–1091.
- Asmussen, M., 1979. Density-dependent selection. II. The Allee effect. *Am. Nat.* 114, 796–809.
- Berec, L., Angulo, E., Courchamp, F., 2007. Multiple Allee effects and population management. *Tree* 22, 185–191.
- Boukal, D.-S., Berec, L., 2002. Single-species models of the Allee effect: extinction boundaries, sex ratios and mate encounters. *J. Theoret. Biol.* 218 (3), 375–394.
- Clutton-Brock, T.-H., et al., 1999. Predation, group size and mortality in a cooperative mongoose, *Suricata suricatta*. *J. Anim. Ecol.* 68 (4), 672–683.
- Courchamp, F., Berec, L., Gascoigne, J., 2008. *Allee Effects in Ecology and Conservation*. Oxford Biology.
- Courchamp, F., Clutton-Brock, T., Grenfell, B., 1999. Inverse density dependence and the Allee effect. *Tree* 14, 405–410.
- Dennis, B., 1989. Allee effect: population growth, critical density, and chance of extinction. *Nat. Resour. Model.* 3, 481–538.
- De Vries, G., Hillen, T., Lewis, M., Müller, J., Schönfisch, B., 2006. *A Course in Mathematical Biology: Quantitative Modeling with Mathematical and Computational Methods*, Vol. 12. SIAM.
- Doebeli, M., 1995. Dispersal and dynamics. *Theor. Popul. Biol.* 47, 82–106.
- Gruntfest, Y., Arditi, R., Dombrovsky, Y., 1997. A fragmented population in a varying environment. *J. Theoret. Biol.* 185, 539–547.
- Gyllenberg, M., Hemminki, J., Tammara, T., 1999. Allee effects can both conserve and create spatial heterogeneity in population densities. *Theor. Popul. Biol.* 56, 231–242.
- Hanski, I., 2001. Spatially realistic theory of metapopulation ecology. *Naturwissenschaften* 88 (9), 372–381.
- Hanski, I., Gilpin, M.-E., 1991. Metapopulation dynamics: brief history and conceptual domain. In: Gilpin, M.-E., Hanski, I. (Eds.), *Metapopulation Dynamics: Empirical and Theoretical Investigations*. Academic Press, London, pp. 3–16.

- Hastings, A., 1993. Complex interactions between dispersal and dynamics: Lessons from coupled logistic equations. *Ecology* 74, 1362–1372.
- Holt, R.-D., 1985. Population dynamics in two-patch environments: Some anomalous consequences of an optimal habitat distribution. *Theor. Popul. Biol.* 28, 181–208.
- Hopf, F.-A., Hopf, F.-W., 1985. The role of the Allee effect in species packing. *Theor. Popul. Biol.* 27, 27–50.
- Kang, Y., Lanchier, N., 2011. Expansion or extinction: deterministic and stochastic two-patch models with Allee effects. *J. Math. Biol.* 62 (6), 925–973.
- Keitt, T.-H., Lewis, M.-A., Holt, R.-D., 2001. Allee effects, invasion pinning, and species' borders. *Am. Nat.* 157, 203–216.
- Krantz, S.-G., Parks, H.-R., 2012. *The Implicit Function Theorem: History, Theory, and Applications*. Springer Science & Business Media.
- Levin, S.-A., 1974. Dispersion and population interactions. *Am. Nat.* 108, 207–228.
- Levin, S.-A., Segel, L.-A., 1985. Pattern generation in space and aspect. *SIAM Rev.* 27, 45–67.
- Levins, R., 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. *Bull. Entomol. Soc. Am.* 15, 237–240.
- Levins, R., 1970. Extinction. In: Gerstenhaber, M. (Ed.), *Some Mathematical Problems in Biology*. Mathematical Society, Providence, R.I., pp. 77–107.
- Lewis, M.-A., Kareiva, P., 1993. Allee dynamics and the spread of invading organisms. *Theor. Popul. Biol.* 43, 141–158.
- MacArthur, R.-H., Wilson, E.-O., 1963. An equilibrium theory of insular zoogeography. *Evolution* 17, 373–387.
- MacArthur, R.-H., Wilson, E.-O., 1967. *The Theory of Island Biogeography*. Princeton University Press, Princeton.
- Odum, E., Barrett, G.-W., 2004. *Fundamentals of Ecology*. Thomson Brooks/Cole, Belmont, CA.
- Poethke, H.-J., Hovestadt, T., 2002. Evolution of density- and patch-size-dependent dispersal rates. *Proc. R. Soc. Lond. Ser. B: Biol. Sci.* 269 (1491), 637–645.
- Ruxton, G., 1993. Linked populations can still be chaotic. *Oikos* 68, 347–348.
- Ruxton, G., 1994. Low levels of immigration between chaotic populations can reduce system extinctions by inducing asynchronous regular cycles. *Proc. R. Soc. Lond. Ser. B* 256, 189–193.
- Sinclair, A.-R.-E., et al., 1998. Predicting effects of predation on conservation of endangered prey. *Conserv. Biol.* 12 (3), 564–575.
- Stephens, P.-A., Sutherland, W.-J., 1999. Consequences of the Allee effect for behaviour, ecology and conservation. *Trends Ecol. Evolut.* 14 (10), 401–405.
- Yakubu, A.-A., Castillo-Chavez, C., 2002. Interplay between local dynamics and dispersal in discrete-time metapopulation models. *J. Theoret. Biol.* 218 (3), 273–288.