

Spatially heterogeneous populations with mixed negative and positive local density dependence

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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.

Keywords: patch-model. Allee effect. population migration. ODE.

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

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

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36 size of the population can be expressed by the difference of births and deaths. If
37 environmental conditions are favourable (that is, food, space, etc. are abundant),
38 then the population is able to grow. Growth is said to be exponential when the
39 growth rate is proportional to the total population size. However, when resources
40 are limited, an intraspecific competition of the individuals can occur which results
41 in a slowdown of the exponential growth as competition for the resources increases.
42 Eventually, population growth decreases nearly to zero as the population reaches
43 the carrying capacity of the environment. This way, the growth of the population is
44 described by an S-shaped curve, known as the logistic curve.

45 Numerous examples illustrate that in real ecosystems the growth of populations
46 can exhibit another type of dynamics, the Allee effect, which is very different from
47 that of exponential and logistic growth. Animal populations are often subject to the
48 Allee effect, that is, they are better able to grow at higher densities. The concept was
49 first described by Warder Clyde Allee, who studied the growth of goldfish. While
50 classical population dynamics modelling approaches – including the concepts of ex-
51 ponential and logistic growth – assume negative density dependence of per capita
52 growth rate, Allee’s experiments showed that goldfish were better able to survive
53 on higher densities. It has been observed that certain aquatic species can affect the
54 chemistry of the water by releasing protective chemicals that could enhance their
55 survival. In a tank, goldfish better manage to render the water closer to their op-
56 timal chemical requirements when there are several of them (Allee et al, 1932 [1]).
57 Based on his experiments and observations, Allee arrived to the conclusion that the
58 evolution of social structures is not only driven by competition (which classically
59 implies negative density dependence), but that cooperation is another fundamental
60 principle in animal species (Allee, 1931 [2]). The individuals of many species coop-
61 erate in various ways: they join forces to hunt or to escape predators, they forage
62 together, they use cooperative strategies to survive unfavourable conditions, or they
63 seek partners for reproduction.

64 The phenomenon of the Allee effect, often referred to as positive density de-
65 pendence in population growth, has been studied comprehensively in the literature.
66 Both in the direction of theoretical works with mathematical models and empirical
67 works with the unveiling of Allee dynamics in natural populations, a large number
68 of studies have been published (Dennis, 1989 [3]; Courchamp et al, 1999 [4]; Berec
69 et al, 2007 [5], Stephens and Sutherland, 1999 [6]). We also refer to the excellent
70 book of Courchamp, Berec, and Gascoigne, 2008 [7] which details the history and
71 recent developments of the topic, and also provides a thorough overview of the rel-
72 evant literature. We distinguish two types of Allee effect: the strong and the weak
73 Allee effects. The strong Allee effect includes a population threshold that is often
74 referred to as the Allee threshold: the population goes extinct when rare (per capita
75 growth rate is negative), and it is able to grow at densities higher than the thresh-
76 old (Dennis, 1989 [3]; Lewis and Kareiva, 1993 [8]; Odum and Barrett, 2004 [9]). In
77 case when a weak Allee effect occurs in the population, the per capita population
78 growth rate is lower (however, still positive) at low densities than at higher densities.

79
80 An Allee effect can arise from a large variety of different ecological mechanisms.
81 There are several types of reproductive Allee effects, as fertilization efficiency in ses-
82 sile organisms, mate finding in mobile organisms or cooperative breeding. Examples
83 also include mechanisms related to survival, like environmental conditioning and

84 predation. Comprehensive description of the various mechanisms with appropriate
85 ecological examples can be found in Berec et al, 2007 [5]; Stephens and Sutherland,
86 1999 [6]; Courchamp et al, 2008 [7]. Predation can generate a strong Allee effect in
87 prey. An example for this mechanism is the case of the island fox (prey) and the
88 golden eagle (predator) on the California Channel Islands (Angulo et al, 2007 [10]).
89 Foxes are consumed by eagles as secondary prey, since feral pigs are the main prey
90 for eagles. If pigs are not present on an island, then eagles won't sustain a permanent
91 population on that habitat, as the fox population by itself cannot provide enough
92 prey. If, on the other hand, there are sufficient pigs around to maintain the eagle pop-
93 ulation then the eagles establish residence on the island. This way, eagle population
94 dynamics do not depend on fox density, and unlike in the classical predator-prey
95 models, eagles can deplete the fox population without negative feedback on the
96 predator population. If the eagle kill rate follows a Holling type II functional re-
97 sponse then this phenomenon reveals an Allee effect in the fox population, since the
98 lower the fox density, the higher the individual risk of eagle predation (Angulo et
99 al, 2007 [10]). Clutton-Brook et al, 1999 [11] also compared survival between prey
100 populations living in sites where predators are abundant and sites where predators
101 have been reduced or removed as a result of human interference. They find that suri-
102 cates in Kalahari Gemsbok Park—an area of high predator density—were subject to a
103 strong Allee effect whilst those living in the neighbouring ranchland where predator
104 density is relatively low, could survive even in small groups.

105 If the mechanism that triggers the Allee effect depends on ecological circum-
106 stances (e.g., presence of particular predators), then the Allee effect may be present
107 in some areas or time periods, and absent in others. Sinclair et al, 1998 [12] investi-
108 gates the impact of reintroducing endangered predators on the prey. Since predation
109 causes an Allee effect in the prey population which is not the primary food supply
110 for the predator, it might be necessary to apply predator control to allow the escape
111 of the prey population. In Australia, several indigenous mammals—the black-footed
112 rock wallaby and the quokka for instance—have been reduced to a fraction of their
113 former range, so for their conservation some sensitive prey species are now con-
114 fined to outer islands where exotic predators (feral cats and red foxes) are absent.
115 Sometimes different habitats support different colony sizes, and it depends on their
116 density whether the population is subject to an Allee effect or grows logistically.
117 Pollock apply two types of strategies for protection from predators. Fish who live in
118 structured habitats (such as algal beds) disperse to reduce detection by predators,
119 so predation triggers a negative density dependence in fish. On the other hand, in
120 open intertidal habitats the fish shoal, which means that their risk-dilution effect is
121 positively density dependent (Stephens et al, 1999 [6]).

122
123 The term “metapopulation” was introduced in the works of Richard Levins in
124 1969 [13] and 1970 [14], referring to a collection of local populations that are con-
125 nected by migration ([14]). The metapopulation concept, though it has undergone
126 some paradigm shift, has been firmly established in population ecology and conser-
127 vation biology since the work of Gilpin and Hanski, 1991 [15], and the topic is also
128 receiving increasing attention in mathematical modelling of ecological processes.
129 The classical metapopulation theory (Levins, 1969 [13]) rests on the assumptions
130 that dynamics of local populations occur on a fast time scale in comparison with
131 metapopulation dynamics. This way, the classical metapopulation theory is con-

132 cerned with the number of local populations but changes in their sizes is ignored.
133 The dynamic theory of island biogeography (MacArthur and Wilson, 1963 [16], 1967
134 [17]), models the changes in the size of local population in the discrete habitat frag-
135 ments (patches). In a mathematical model that rests on the island theory approach
136 the dynamic variable is the number of individuals on a particular patch, while in the
137 classical approach the dynamic variable is the number of habitat fragments occupied
138 by the species. Hanski, 2011 [18] explains how the two metapopulation approaches
139 can be integrated by providing a theoretical framework that explicitly unites the
140 two theories.

141

142 In this paper we focus on the approach where the size of local populations is
143 modelled. Most literature with this approach assume negatively density-dependent
144 (typically, logistic) growth in the local populations ([13, 14, 19, 20, 21, 22, 23, 24,
145 25, 26, 27]). Besides, spatial theory for the case when the local dynamics is governed
146 by the Allee effect is also relatively well developed ([3, 7, 8, 28, 29, 30, 31, 32]).
147 However, an interesting question—that hasn't been studied yet—is how dispersal and
148 spatial heterogeneity influence metapopulation dynamics when the nature of local
149 density-dependence is negative in some patches but positive in others. Throughout
150 the above discussion we provided examples for real animal metapopulations where
151 in some habitats local populations grow logistically while different locations exhibit
152 an Allee effect. Such difference in the local dynamics can arise when some ecological
153 circumstances (e.g., presence of particular predators) vary over the localities.

154 We consider an animal population distributed over several discrete geographical
155 patches that are interconnected by dispersal. If a local population is subject to a
156 strong Allee effect then typically it has three steady states: the extinction (zero) equi-
157 librium attracts every solution started below a positive equilibrium (Allee threshold,
158 unstable), and all solutions converge to the population carrying capacity (another
159 positive, stable equilibrium) if the initial population size is larger than the Allee
160 threshold. On the other hand, in a local population that follows logistic growth
161 there exist only two steady states: the extinction equilibrium is unstable, while the
162 positive steady state—representing population carrying capacity—is globally stable.
163 Studying the dynamics of animal population where density dependence varies over
164 spatial locations hasn't received much attention despite the numerous examples in
165 real ecosystems ([6, 10, 11, 12]). Here we show that if some of the patches are subject
166 to a strong Allee effect then many steady states exist. Our accurate mathematical
167 description characterizes the structure and the stability of the equilibria in terms of
168 local density dependence and the migration routes between the patches. Due to the
169 coexistence of many positive stable steady states, making predictions for the future
170 behaviour of such systems can be rather challenging.

171 1 Mathematical model

172 We consider r patches, and denote the population of patch i at time t by $N_i(t)$
173 for $i = 1, \dots, r$ and $t \geq 0$. Population growth at patch i is modelled by the term
174 $N_i \cdot g_i(N_i)$ in an ordinary differential equation. This formulation immediately implies
175 that each patch has an extinction state. We assume that g_i is $r - 1$ times continu-
176 ously differentiable for each $i \in \{1, \dots, r\}$, and consider two different scenarios for
177 population growth in the patches. We assume that for s patches ($0 \leq s \leq r$) the

178 population is subject to a strong Allee effect, while the population growth is given
 179 by the logistic function for the remaining $r - s$ patches. To model this, we assume
 180 that g_a ($a \leq s$) has two zeros: one gives the unstable Allee threshold \bar{A}_a (sometimes
 181 also called the extinction threshold), and another corresponds to the stable carrying
 182 capacity \bar{K}_a ; and we assume that g_b ($s + 1 \leq b \leq r$) has only one zero, representing
 183 the stable carrying capacity \bar{K}_b of the patch. This is formulated mathematically as

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

184 where $0 < \bar{A}_a < \bar{K}_a$ for $a \leq s$. Furthermore, we assume that $g_a(0) < 0$ when $a \leq s$
 185 and $g_b(0) > 0$ when $s + 1 \leq b \leq r$, that is, the extinction steady state of a patch
 186 is asymptotically stable if a strong Allee effect can occur in the population, and
 187 unstable for a patch with logistic population growth. Logistic population growth
 188 is typically modelled with $g_b(N_b) = r_b(\bar{K}_b - N_b)$, and numerous examples for the
 189 mathematical formulations of the Allee effect can be found in the literature that
 190 satisfy our general assumptions on g_a , e.g. $g_a(N_a) = r_a(\bar{K}_a - N_a)(N_a - \bar{A}_a)$ ([3, 28,
 191 33, 34, 35, 36]).

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

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

198 Standard results from the theory of differential equations [37] guarantee that the
 199 system is well-posed. We denote our model by (M_0) in the special case when there is
 200 no spatial dispersal between the patches, that is, $\alpha = 0$ and the habitats are isolated.

201 **2 Extinction equilibrium and steady states where** 202 **all local populations are abundant**

203 Equilibria of the model (M_α) arise as solutions of the steady state system

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

204 One immediately derives the following result, that holds for any α and c^{ij} ($i, j \in$
 205 $\{1, \dots, r\}$, $i \neq j$).

206 **Theorem 2.1.** *The system (M_α) has a steady state that corresponds to extinction*
 207 *in all habitats.*

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

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

210 where we see that the equations decouple, and solving the system requires solving
 211 r scalar equations which are pairwise independent. There are s patches that exhibit
 212 a strong Allee effect and each has 3 equilibria, moreover all r patches with logistic
 213 growth have 2 steady states; therefore, there are $3^s \cdot 2^{r-s}$ equilibria in the system
 214 (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
 215 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 $s + 1 \leq b \leq r$.

216 Whereas finding the solutions is fairly trivial in the case of isolated patches, solv-
 217 ing the steady state system (2) can be very difficult and sometimes impossible when
 218 dispersal is incorporated. However, by knowing the roots of (2) without dispersal,
 219 the implicit function theorem (see [38] for reference) enables us to retrieve some in-
 220 formation on the steady states for small values of dispersal. To this end, we rewrite
 221 the system (M_α) in the compact form

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

222 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
 223 defined as the right hand side of the i th equation of the system (M_α) , $i \in \{1, \dots, r\}$.
 224 Note that (3) is equivalent to (M_0) in the special case when $\alpha = 0$.

225 The steady state system (2) can be formulated as $\mathcal{T}(\alpha, \mathcal{X}) = 0$. When the patches
 226 are isolated then this equation reads $\mathcal{T}(0, \mathcal{X}) = 0$, and we have a perfect understand-
 227 ing of the roots. To apply the implicit function theorem, we note that \mathcal{T} is an $r - 1$
 228 times continuously differentiable function on $\mathbb{R} \times \mathbb{R}^r$, and the matrix $(\frac{\partial \mathcal{T}}{\partial \mathcal{X}})(0, \bar{N}^0)$
 229 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
 230 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
 231 nonzero. The implicit function theorem then says:

232

233 *Consider an equilibrium \bar{N}^0 of the model (M_0) . There exists a positive constant*
 234 *α_E , an open set U_E containing \bar{N}^0 , and a unique $r - 1$ times continuously differ-*
 235 *entiable 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*
 236 *$\mathcal{T}(\alpha, \bar{N}(\alpha)) = 0$ for $\alpha \in [0, \alpha_E)$.*

237

238 We arrive at the following result.

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

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

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

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

258 3 Mixed steady states with extinct, rescued or abun- 259 dant local populations

260 Other than the extinction steady state and componentwise positive equilibria, the
 261 system (M_0) also has equilibria with mixed zero and positive components. In fact, in
 262 (M_0) there are $3^s \cdot 2^{r-s} - 1 - 2^s$ such boundary equilibria (which is the total number
 263 minus the zero equilibrium minus the ones with all components being positive),
 264 that correspond to situations when in the absence of spatial dispersal, some local
 265 populations are at positive states while other patches are at zero state. Now we
 266 consider such a steady state \bar{N}^0 of the system (M_0) of isolated local populations.
 267 A boundary equilibrium of (M_0) might disappear when spatial dispersal between
 268 the patches is introduced: mathematically speaking, for some $\alpha > 0$ the unique
 269 continuous function $\bar{N}(\alpha)$ associated with \bar{N}^0 may have negative components. In
 270 other words, the boundary equilibrium moves out from the non-negative cone and
 271 hence it doesn't give a biologically meaningful steady state. On the other hand,
 272 $\bar{N}(\alpha) \geq 0$ means that the boundary equilibrium \bar{N}^0 of (M_0) is preserved for small
 273 values of dispersal.

274 In what follows we describe a mathematical procedure to decide whether a fixed
 275 point $\bar{N}(\alpha)$ associated to a boundary equilibrium of (M_0) , gives a biologically mean-
 276 ingful steady state in the system (M_α) . Applying the procedure to each of the
 277 $3^s \cdot 2^{r-s} - 1 - 2^s$ boundary equilibria of (M_0) , will allow us to give a lower esti-
 278 mate on the number of steady states in (M_α) (equilibria other than those associated
 279 to boundary equilibria of (M_0) , may also arise with dispersal). We introduce some
 280 notation for convenience.

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

- 282 • 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
 283 (Extinct in the Absence of spatial Dispersal) in \bar{N}^0 .
- 284 • If a patch j is occupied in \bar{N}^0 (that is, $\bar{N}_j^0 > 0$), then we say that patch j is
 285 OAD (Occupied in the Absence of spatial Dispersal) in \bar{N}^0 .

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

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

- 291 • If $\frac{d\bar{N}_i}{d\alpha}(0) > 0$ holds for every EAD patch i then $\bar{N}(\alpha)$ is positive if α is small,
 292 that is, for small α the function $\bar{N}(\alpha)$ gives a positive steady state in the system
 293 (M_α) .
- 294 • 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
 295 any small α , which means that the function $\bar{N}(\alpha)$ doesn't give a biologically
 296 meaningful steady state in the system (M_α) .

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

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

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

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

300 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 $g_i(0) \neq 0$,
 301 so we derive the following equation for the derivative, when i is an EAD patch:

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

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

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

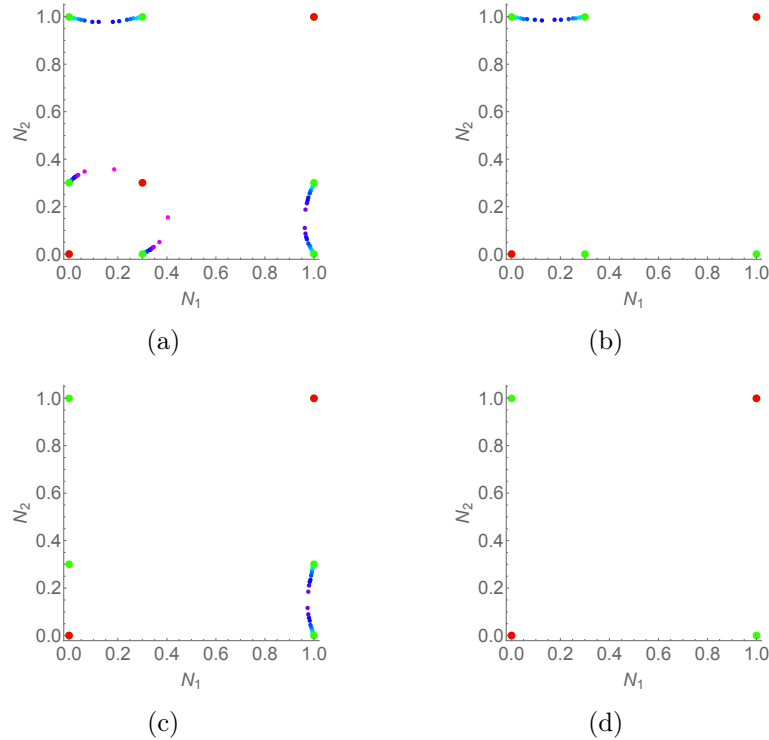


Figure 1: **Structure of steady states in the model (M_α) for two patches, when individuals can move from patch 1 to 2, and from patch 2 to 1 (that is, the migration network forms a complete graph).** In Figure (a) both patches are subject to a strong Allee effect, (b) patch 1 is subject to a strong 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 color 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, $r_1 = 1$, $r_2 = 1.3$, $c^{12} = 1$, $c^{21} = 1$, $\bar{K}_1 = 1$, $\bar{K}_2 = 1$, $\bar{A}_1 = 0.3$, $\bar{A}_2 = 0.3$.

319 Spatial dispersal of populations is influenced by numerous environmental factors,
320 as distance between habitats, fitness of individuals, or human interference that limit
321 accessibility of certain geographic areas. One can think of various reasons why two
322 habitats are not connected, or are connected by a one-way route only. In our math-
323 ematical model, such a scenario is implemented by setting one or more connectivity
324 potential parameters to zero. If $c^{ij} = 0$ holds, then no individual migrates from

325 patch j to i directly (however, this doesn't necessarily mean that i is unreachable
326 from j as there may exist an indirect way via other locations). When investigating
327 whether a fixed point $\bar{N}(\alpha)$ associated to a boundary equilibrium \bar{N}^0 of (M_0) gives
328 a biologically meaningful steady state in the system (M_α) with spatial dispersal, we
329 look at the derivative of the function at all patches that are extinct without dispersal
330 (see Remark 3.2). By equation (4), such derivatives are non-zero as long as the sum
331 in the numerator of (4) is non-zero, that is,

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

332 We remind that, speaking of a boundary equilibrium with mixed positive and zero
333 components, there always exists a j such that \bar{N}_j^0 is positive. Thus, if $c^{ij} > 0$ for all
334 j (migration to i is possible from any other patch directly), or $\bar{N}_j^0 > 0$ and $c^{ij} > 0$
335 hold at the same time, then the derivative of \bar{N}_i is non-zero, and one can easily
336 decide whether $\bar{N}_i(\alpha)$ is positive or negative for small α . On the other hand, it is
337 also possible that $c^{ij} = 0$ whenever $\bar{N}_j^0 > 0$, meaning that there is no direct way to i
338 from patches that are at positive steady state (occupied) in the absence of dispersal.
339 In such case, equation (4) is not sufficient to decide whether the fixed point $\bar{N}(\alpha)$
340 associated to the boundary equilibrium \bar{N}^0 , gives a biologically meaningful steady
341 state in the system (M_α) , since the derivative of \bar{N}_i is zero.

342 To overcome this difficulty, one has to look at higher order derivatives and the
343 entire network of connections between patches, instead of just looking at locations
344 that directly connect to EAD patches. We give Theorem 3.4 below to show that
345 our earlier result in Theorem 3.3 for the special case of a fully connected migration
346 network can be extended to general migration networks. Theorem 3.4 is applicable
347 to an arbitrary connection network between the patches, hence the proof is much
348 more technical than the one for the fully connected migration network in Theorem
349 3.3. For this reason, we refer the interested reader to the Appendix for the proof,
350 nevertheless present Figure 2 for the illustration of the result.

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

357 See Figure 2 below for the equilibria in the model (M_α) in the case when two
358 patches are considered, but patch 1 is not reachable from patch 2. A migration
359 network of five patches is presented in Figure 3. If local populations are isolated
360 then the system has $3^2 \cdot 2^3 = 72$ equilibria, 4 of those are stable and the other 68
361 are unstable. Following the method described in Theorems 2.1, 2.2, and 3.4, one can
362 derive that there are 72 fixed points in the system with small migration values, each
363 associated to an equilibrium of isolated local populations; however, 59 of these fixed
364 points don't give biologically meaningful equilibria, and the system of five patches
365 has 4 stable and 9 unstable steady states for small values of dispersal. In the caption

366 of Figure 3 we show through two examples how to apply the procedure described in
 367 Theorem 3.4.

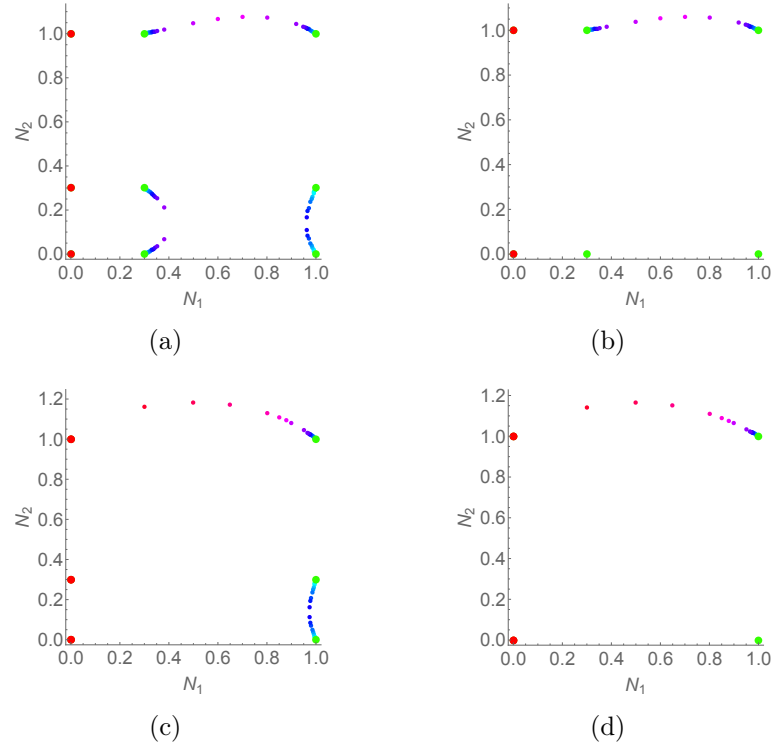


Figure 2: **Structure of steady states in the model (M_α) for two patches, when individuals can move from patch 1 to 2, but they cannot from patch 2 to 1.** In Figure (a) both patches are subject to a strong Allee effect, (b) patch 1 is subject to a strong Allee effect and growth is logistic in patch 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 $g_a(N_a) = r_a(\bar{K}_a - N_a)(N_a - \bar{A}_a)$ for Allee patches and $g_b(N_b) = r_b(\bar{K}_b - N_b)$ for patches with logistic growth, $r_1 = 1$, $r_2 = 1.3$, $c^{12} = 0$, $c^{21} = 1$, $\bar{K}_1 = 1$, $\bar{K}_2 = 1$, $\bar{A}_1 = 0.3$, $\bar{A}_2 = 0.3$.

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

374 4 Discussion

375 We illustrated that populations in a patchy environment can have a large number
 376 of steady states if a strong Allee effect can occur in some of the habitats. We gave

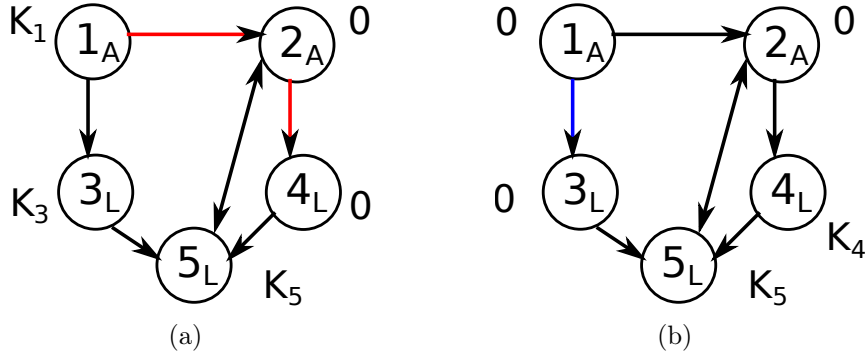


Figure 3: **Migration network of five patches, where patches 1 and 2 exhibit a strong Allee effect, and patches 3, 4, and 5 follow logistic growth.** The migration pathways are indicated by arrows. In the absence of dispersal, such network of patches has 4 stable and 68 unstable steady states, but only 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.

377 a general mathematical model for the dynamics of a single species when individuals
 378 migrate between r patches that can exhibit two types of local density dependence.
 379 Logistic growth and a strong Allee effect are typical examples for negative and
 380 positive density dependence, respectively; however, due to the general formulation
 381 of the local growth function $N_i \cdot g_i(N_i)$, our model is applicable to a broad range of
 382 scenarios for local growth.

383 After understanding the dynamics of local populations, it is easy to describe all
 384 the steady states and their stability when the locations are isolated. If s patches
 385 exhibit a strong Allee effect (having 3 equilibria each) and $r - s$ patches follow
 386 logistic growth (having 2 equilibria each), then the system of disconnected patches
 387 has a total number of $3^s \cdot 2^{r-s}$ equilibria, because from each patch we can choose one
 388 possibility independently. An equilibrium is stable if each component is stable in the
 389 corresponding local dynamics, and the equilibrium is unstable otherwise. Thus, there
 390 are 2^s stable steady states in the combined population of isolated local populations.
 391 On the other hand, finding the steady states in the system with dispersal is difficult.
 392 In this paper, we provided a procedure that describes the structure and stability of
 393 the steady states for small values of migration between the patches. If the migration
 394 network is fully connected, then we found that there are 3^r steady states if all patches
 395 exhibit a strong Allee effect ($s = r$), and there exist $3^s + 1$ equilibria if there is at
 396 least one habitat where growth is logistic ($s < r$). Thus, there exists a large number

397 of steady states and this number grows exponentially in the number of locations. But
398 more importantly, the same statement holds for the number of stable equilibria: for
399 fully connected locations there exist 2^s ($s \leq r$) stable steady states when dispersal
400 rates are low. Calculating these numbers for a general migration network (that is,
401 when some patches don't directly connect) is more challenging, and requires the
402 application of the procedure described in Theorems 2.1, 2.2, and 3.4. These results
403 rest on the idea of finding steady states in the system for low dispersal rates by using
404 our knowledge on the steady states of the system without dispersal. More precisely,
405 the procedure identifies equilibria of the system with dispersal that are close to an
406 equilibrium of the system of isolated locations.

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

419 Amarasekare, 1998 [28] studied the interaction between local dynamics and dis-
420 persal on population persistence in a two-patch model. She found that two local
421 populations that grow logistically are unlikely to go extinct even when rare. Our
422 results for multiple patches with logistic growth agree with those in [28]. We showed
423 that the only stable equilibrium is the one with all local populations at their carrying
424 capacities, whereas all other steady states (if any) are unstable, implying that rare
425 populations are likely to increase. When patches are isolated and all follow Allee dy-
426 namics, then the population goes extinct when rare because rare local populations
427 go to their stable extinction states. Amarasekare, 1998 [28] showed that dispersal
428 leads to a qualitative change in the two-patch system, that is, a patch below the
429 Allee threshold is rescued from extinction by immigrants from another patch that
430 is above the Allee threshold. Our findings for multiple patches are in accordance
431 with this result, in fact, we can say much more. If all local populations exhibit a
432 strong Allee effect then we showed that there are numerous equilibria including a
433 large number of stable steady states. In particular, if a patch is at the extinction
434 steady state in the isolated system, then immigration from another patch that is
435 at positive state, pushes the extinction state to some positive value, thereby the
436 extinct patch becomes occupied. More importantly, the extinction state of a patch
437 with Allee growth is stable in the local dynamics, which means that weak dispersal
438 creates stable positive equilibria that don't exist without dispersal, and this way
439 local populations won't go extinct even if near the extinction state. Our results gen-
440 eralize those by Amarasekare since we consider animal populations where growth
441 can vary over the locations.

442 Regardless of the way local populations grow, the total population of isolated
443 localities has a single componentwise positive stable equilibrium, that corresponds
444 to the patch-wise carrying capacities. In this paper, we showed that a large number

445 of alternate positive stable steady states can exist if some of the patches exhibit a
 446 strong Allee effect. From the dynamical systems perspective, such rich structure of
 447 stable steady states goes hand in hand with complicated behaviour of the model,
 448 that makes predicting the population dynamics particularly difficult.

449 Appendix

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

452
 453 Remark 2.3 cares for the local stability of equilibria of the system (M_α) . To this
 454 end, we investigate the eigenvalues of the Jacobian of the system (2) evaluated at
 455 the equilibria. If all eigenvalues of the Jacobian have negative real parts then the
 456 equilibrium is locally asymptotically stable whereas it is unstable if there is an eigen-
 457 value with positive real part. If local populations are isolated (that is, $\alpha = 0$) then
 458 the equations of (2) decouple, and the Jacobian is a diagonal matrix with diagonal
 459 elements $\frac{d}{dN_i}(N_i \cdot g_i(N_i))$, $i = 1, \dots, r$. Thus, eigenvalues arise as the elements in
 460 the diagonal, and the stability of an equilibrium \bar{N}^0 of the system (M_0) for isolated
 461 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
 462 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
 463 $i = 1, \dots, r$, 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)
 464 and the discussion afterwards we described the steady states of local populations as
 465 well as the stability of these steady states. Note that in the local dynamics, a negative
 466 derivate corresponds to stability whereas a positive derivate means instability.

467 In particular, the extinction equilibrium of the system (M_α) is stable if all patches
 468 exhibit a strong Allee effect ($s = r$), and unstable otherwise. An equilibrium \bar{N}^0
 469 where all patches are occupied, is stable if all local populations are at the carrying
 470 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
 471 unstable otherwise (that is, if there is an a such that $\bar{N}_a^0 = \bar{A}_a^0$). An equilibrium \bar{N}^0
 472 with some local populations at the extinction state and others abundant, is stable
 473 if all patches with logistic growth are at their carrying capacities and patches that
 474 are subject to a strong Allee effect, are either extinct or at their carrying capacities
 475 (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 $b \geq s + 1$).

476 We showed that the steady state system (2) can be obtained in the compact form
 477 $\mathcal{T}(\alpha, \mathcal{X}) = 0$, where α is the general dispersal parameter and $\alpha = 0$ means isolated
 478 local populations. The Jacobian $\frac{d\mathcal{T}}{d\mathcal{X}}(\alpha, \mathcal{X})$ is continuous in α and so is the function
 479 $\bar{N}(\alpha)$, representing an equilibrium of the system (M_α) on the interval $[0, \alpha_E)$ for
 480 small α_E . We remind that the system (2) is equivalent to the system (M_0) when
 481 $\alpha = 0$, so by continuity of eigenvalues with respect to parameters, we arrive to the
 482 statement of Remark 2.3.

483
 484 For the proof of Theorem 3.4, we make the following preparation.

485 **Lemma 4.1.** *For any positive integer n such that $n \leq r - 1$, it holds that*

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

486 whenever patch i ($i \in \{1, \dots, r\}$) is EAD in the boundary equilibrium \bar{N}^0 , and
 487 $\frac{d^l \bar{N}_i}{d\alpha^l}(0) = 0$ for every $l < n$.

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

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

490 Here we used the assumption that g_i is $r-1$ times continuously differentiable. Clearly
 491 $\frac{d^{n-l}(\alpha c^{ij})}{d\alpha^{n-l}} = 0$ whenever $n-l \geq 2$, moreover $\frac{d(\alpha c^{ij})}{d\alpha} = c^{ij}$, so if $\frac{d^l \bar{N}_i}{d\alpha^l}(0) = 0$ holds for
 492 all $l < n$ then (5) at $\alpha = 0$ reads

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

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

494 **Definition 4.2.** Consider a patch i that is EAD in the boundary equilibrium \bar{N}^0 .
 495 We define D_i as the least nonnegative integer such that in the migration network,
 496 there is a path that starts with an OAD patch j , ends with patch i , and contains D_i
 497 patches in-between. If there is no such path then let $D_i = r-1$.

498 **Definition 4.3.** We characterize connectivity between patches.

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

505 **Lemma 4.4.** If i is an EAD patch in \bar{N}^0 , then it holds that $\frac{d^l \bar{N}_i}{d\alpha^l}(0) = 0$ whenever
 506 $l \leq D_i$.

507 *Proof.* Indeed, the inequality $D_{i_0} \geq 0$ is satisfied for every patch i_0 with $\bar{N}_{i_0} = 0$.
 508 The case when $D_{i_0} = 0$ is trivial, so we consider a patch i_1 for which $D_{i_1} \geq 1$, and
 509 from Lemma 4.1 we derive

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

510 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
 511 right hand side is zero. We obtain that $\frac{d\bar{N}_{i_1}}{d\alpha}(0) = 0$.

512 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
 513 $D_{i_2} \geq 2 \geq 1$, so Lemma 4.1 yields the equation

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

514 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
 515 follows that $D_j \geq 1$, henceforth $\frac{d\bar{N}_j}{d\alpha}(0) = 0$ holds by induction, and the right hand
 516 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
 517 where $D_{i_2} \geq 2$.

518 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
 519 $D_{i_l} \geq l$ holds. This proves the lemma. \square

520 **Theorem 4.5.** *Assume that in the boundary equilibrium \bar{N}^0 , there is a patch i that*
 521 *is EAD and growth is logistic, furthermore i is reachable from an OAD patch. Then*
 522 *there is an $\alpha^* > 0$ such that $\bar{N}^i(\alpha) < 0$ for $\alpha \in (0, \alpha^*)$, which implies that $\bar{N}(\alpha)$*
 523 *has a negative component and it doesn't give a biologically meaningful equilibrium in*
 524 *(M_α).*

525 *Proof.* The proof is by contradiction. Assume that \bar{N}^0 is such that there are patches
 526 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
 527 is reachable from i_+ , and there exists an $\alpha^{**} > 0$ such that $\bar{N}(\alpha) \geq 0$ on $[0, \alpha^{**}]$.
 528 If patches i_0 and i_+ –as described above– exist then there is a minimal distance
 529 between such patches, i.e., there exists a least nonnegative integer $L \leq r - 2$ such
 530 that there is a path from an OAD patch via L patches to a patch which is EAD in
 531 \bar{N}_0 and with logistic growth. We denote by i this patch in the shortest path, and
 532 let i_{L+1}^* be the OAD patch.

533 In the case when $L = 0$, Lemma 4.1 immediately yields contradiction. Indeed,
 534 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
 535 equation

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

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

541 By Lemma 4.1, $\bar{N}_{i_L^*}^0 = 0$ yields

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

542 The equation has a positive right hand side since $\overline{N}_{i_{L+1}^*}^0 = \overline{N}_{i_{L+1}^*}(0) > 0$ and $g_{i_L^*}(0) <$
 543 0 , which implies that $\frac{d\overline{N}_{i_L^*}}{d\alpha}(0) > 0$. A similar equation

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

544 follows from $\overline{N}_{i_{L-1}^*}^0 = 0$ and Lemma 4.1. We note that $D_{i_{L-1}^*} = 1$, hence $\overline{N}_j(0) = 0$
 545 holds for every j such that $c^{i_{L-1}^*,j} \neq 0$. The zero numerator yields $\frac{d\overline{N}_{i_{L-1}^*}}{d\alpha}(0) = 0$, so
 546 we can apply Lemma 4.1 to derive

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

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

552 Next, we consider patch i_{L-2}^* , where $D_{i_{L-2}^*} = 2$. For any patch j for which
 553 $c^{i_{L-2}^*,j} \neq 0$, it holds that $D_j \geq 1$, thus $\overline{N}_j(0) = 0$ and $\frac{d\overline{N}_j}{d\alpha}(0) = 0$ hold by Lemma
 554 4.4. Thus, the right hand side of equation

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

555 is zero, so it follows that $\frac{d\overline{N}_{i_{L-2}^*}}{d\alpha}(0) = 0$, and thus Lemma 4.1 yields

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

556 We obtain again that $\frac{d^2\overline{N}_{i_{L-2}^*}}{d\alpha^2}(0) = 0$ since all derivatives in the right hand side are
 557 zero. Finally, by Lemma 4.1 we derive

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

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

562 Following these arguments, one can prove that $\frac{d^{m+1}\bar{N}_{i^*}^{L-m}}{d\alpha^{m+1}}(0) > 0$ for $m =$
563 $0, 1, \dots, L-1$ (we remark that for $m = L-1$ this reads $\frac{d^L\bar{N}_{i^*}}{d\alpha^L}(0) > 0$), and that for
564 any fixed m and $k \leq m$, it holds that $\frac{d^k\bar{N}_{i^*}^{L-m}}{d\alpha^k}(0) = 0$. We note that $D_i = L$, which
565 also means by Lemma 4.4 that $\frac{d^m\bar{N}_i}{d\alpha^m}(0) = 0$ for $m \leq D_i = L$. Henceforth, we can
566 apply Lemma 4.1 and derive

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

567 $D_i = L$ 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
568 satisfied for $m = 0, 1, \dots, L-1$. The assumption that $\bar{N}(\alpha) \geq 0$ for small α yields
569 that $\frac{d^L\bar{N}_j}{d\alpha^L}(0) < 0$ is impossible; this, together with $\frac{d^L\bar{N}_{i^*}}{d\alpha^L}(0) > 0$ and $c^{i,i^*} > 0$,
570 implies the positivity of the numerator. As $g_i(0) > 0$ holds, it follows that $\frac{d^{L+1}\bar{N}_i}{d\alpha^{L+1}}(0)$
571 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
572 $\bar{N}_i(\alpha) < 0$ for small α , a contradiction. The proof is complete. \square

573 **Theorem 4.6.** *Assume that in the boundary equilibrium \bar{N}^0 , there is a strong Allee*
574 *effect in every EAD patch j where $D_j < r-1$. Then for an EAD patch i that is*
575 *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*
576 *$\bar{N}(\alpha) = 0$ if $D_i = r-1$.*

577 *Proof.* If i is at the extinction steady state for $\alpha = 0$, and the patch is not reachable
578 from any patch j with $\bar{N}_j > 0$ (that is, $D_i = r-1$), then no individuals migrate
579 into i when spatial dispersal is incorporated, and hence we have $\bar{N}_i(\alpha) = 0$ for any
580 $\alpha > 0$. In the case when $D_i < r-1$, the proof is by induction. If $D_{i_0} = 0$ for a patch
581 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
582 such that $c^{i_0,j} \neq 0$ and $\bar{N}_j^0 > 0$, so

$$\frac{d\bar{N}_{i_0}}{d\alpha}(0) = -\frac{\sum_{\substack{j=1 \\ j \neq i_1}}^r c^{i_0,j} \bar{N}_j(0)}{g_{i_0}(0)}.$$

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

584 Whenever $D_{i_1} = 1$ is satisfied in a patch i_1 where $\bar{N}_{i_1}^0 = 0$ and subject to a
585 strong Allee effect, Lemma 4.4 implies $\frac{d\bar{N}_{i_1}}{d\alpha}(0) = 0$, so by Lemma 4.1 we derive

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

586 For every j with $c^{i_1,j} \neq 0$ and $1 \leq D_j \leq r-1$, Lemma 4.4 gives $\frac{d\bar{N}_j}{d\alpha}(0) = 0$.
587 If there is a j such that $D_j = 0$, j is EAD and $c^{i_1,j} \neq 0$, then there necessarily
588 is a strong Allee effect in j , so $\frac{d\bar{N}_j}{d\alpha}(0) > 0$ holds by induction. Nevertheless, the
589 positivity of the right hand side of the last equation is guaranteed because we know
590 from $D_{i_1} = 1$ that there must exist a j where $D_j = 0$ and $c^{i_1,j} \neq 0$, hence the
591 inequality $\frac{d^2\bar{N}_{i_1}}{d\alpha^2}(0) > 0$ follows.

592 We assume that the statement of the theorem holds for any EAD patch i that
 593 is subject to a strong Allee effect and $D_i \leq L$, $0 < L < r - 2$. We consider an EAD
 594 patch i_{L+1} where $D_{i_{L+1}} = L + 1$ and there is to a strong Allee effect, and obtain the
 595 equation

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

596 by Lemma 4.1 and Lemma 4.4. $D_{i_{L+1}} = L + 1$ makes $D_j \geq L$ for each j where
 597 $c^{i_{L+1},j} \neq 0$, and from Lemma 4.4 we have $\frac{d^{L+1}\bar{N}_j}{d\alpha^{L+1}}(0) = 0$ for each j where $c^{i_{L+1},j} \neq 0$
 598 and $D_j \geq L + 1$. The case when $D_j = L$ is only possible if j is EAD and subject
 599 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
 600 by induction. There exists a j such that $c^{i_{L+1},j} > 0$ and $D_j = L$, hence the right
 601 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
 602 completes the proof. \square

603 Theorem 4.5 ensures that for a boundary equilibrium $\bar{N}(0) = \bar{N}^0$ of (M_0) , the
 604 point $\bar{N}(\alpha)$ will not be a biologically meaningful fixed point of the system (M_α) if
 605 there is a EAD patch i in \bar{N}^0 where population growth is logistic and i is reachable
 606 from an OAD patch. On the other hand, a boundary equilibrium $\bar{N}(0) = \bar{N}^0$ of (M_0)
 607 will persist for small values of spatial dispersal if in all EAD patches of \bar{N}^0 that are
 608 reachable from an OAD patch, a strong Allee effect can occur. More precisely, in
 609 Theorem 4.6 we show that \bar{N}_i has a positive derivative whenever patch i is EAD,
 610 subject to a strong Allee effect, and reachable from an OAD patch j . Then, by
 611 Lemma 4.4, the statement yields that $\bar{N}_i(\alpha)$ is positive for small α . EAD patches that
 612 are unreachable from OAD patches won't become occupied with the introduction
 613 of spatial dispersal. This last remark, together with Theorems 4.5 and 4.6, proves
 614 Theorem 3.4.

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