

## Quasi-Local Competition in Stage-Structured Metapopulations: A New Mechanism of Pattern Formation

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**Abstract** A central question of ecology is what determines the presence and abundance of species at different locations. In cases of ecological pattern formation, population sizes are largely determined by spatially distributed interactions and may have very little to do with the habitat template. We find pattern formation in a single-species metapopulation model with quasi-local competition, but only if the populations have (at least) two age or stage classes. Quasi-local competition is modeled using an explicit resource competition model with fast resource dynamics, and assuming that adults, but not juveniles, spend a fraction of their foraging time in habitat patches adjacent to their home patch. Pattern formation occurs if one stage class depletes the common resource but the shortage of resource affects mostly the other stage. When the two stages are spatially separated due to quasi-local competition, this results in competitive exclusion between the populations. We find deep similarity between spatial pattern formation and population cycles due to competitive exclusion between cohorts of biennial species, and discuss the differences between the present mechanism and established ways of pattern formation such as diffusive instability and distributed competition with local Allee-effects.

**Keywords** Metapopulation · Pattern formation · Quasi-local competition · Spatially distributed competition · Stage structure

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## 1. Introduction

Biomathematicians have been intrigued by pattern formation ever since the groundbreaking work of Turing (1952). Naive intuition suggests that a homogeneous environment should be uniformly populated. There are, however, striking examples of ecological pattern formation, such as striped vegetation in semiarid areas (Klausmeier, 1999), which show that the environmental symmetry can be broken.

The classic mechanism of pattern formation involves an activator–inhibitor system where the inhibitor diffuses better than the activator (Turing, 1952; see, e.g., Edelstein-Keshet, 1988; Murray, 2003 for detailed introductions and Holmes et al., 1994 for a succinct review of various ways of pattern formation). In an ecological context, this can be realized by a predator–prey system where the predator is more mobile (Segel and Jackson, 1972; De Roos et al., 1998). Pattern formation in homogeneous environments is, however, also possible in single-species systems if two conditions are satisfied (Levin and Segel, 1985; Britton, 1989; Furter and Grinfeld, 1989): First, competition is spatially distributed such that individuals would experience large competitive impact in areas adjacent to existing populations (*lateral inhibition*); and second, Allee-effects enhance population growth in existing populations, but this effect is more localized than competition (*local activation*).

In metapopulations consisting of discrete habitat patches, pattern formation amounts to the destabilization of the homogeneous equilibrium and the stabilization of inhomogeneous equilibria. At an inhomogeneous equilibrium, the habitat patches differ in their equilibrium population density despite the fact that environmental conditions are identical. The analog of distributed competition in discrete metapopulations is termed quasi-local competition, where individuals of one population compete also with members of adjacent populations (Gyllenberg et al., 1999; Doebeli and Killingback, 2003; Kisdi and Utz, 2005). Quasi-local competition results if the resource disperses between neighboring populations such that consumption by one population depletes the resource also of the adjacent populations (Levin, 1974), or if, as in our model, individuals spend a certain fraction of their foraging time in the adjacent populations. “Apparent competition” can also be quasi-local or nonlocal if a mobile predator or parasite regulates population growth (De Roos et al., 1998). In contrast to competition, Allee-effects are assumed to operate only within populations.

Most metapopulation models assume that local populations are connected only by dispersal. Under this assumption, Allee-effects can stabilize existing spatial patterns by preventing population growth in empty habitat patches and thus stabilizing inhomogeneous equilibria (Gruntfest et al., 1997; Amarasekare, 1998). In the absence of lateral inhibition provided by quasi-local competition, however, the homogeneous equilibrium remains locally stable (Gyllenberg et al., 1999). Indeed, Rohani et al. (1996) have proved under rather general conditions that when identical patches are connected only by passive dispersal, the homogeneous equilibrium is stable if and only if the dynamics of a single isolated population has a stable fixed point. Allee-effects (local activation) without quasi-local competition (lateral inhibition) can conserve but cannot generate spatial patterns (Gyllenberg et al., 1999).

Is quasi-local competition sufficient by itself to destabilize the homogeneous equilibrium? Many classic examples show that in order to form patterns, lateral inhibition must be accompanied by some form of local activation, such as Allee-effects from enhanced reproduction or predator saturation, or locally favorable conditions in heterogeneous environments (Segel and Jackson, 1972; Levin, 1974; Gurney and Nisbet, 1976; Levin and Segel, 1985; Britton, 1989; Furter and Grinfeld, 1989; Gyllenberg et al., 1999; Sasaki, 1997; De Roos et al., 1998). In sharp contrast to previous results, however, Doebeli and Killingback (2003) found pattern formation in a metapopulation subject only to quasi-local competition, without any form of local Allee-effects and in a homogeneous environment.

The model of Doebeli and Killingback (2003) contained only one species and incorporated quasi-local competition via an extension of the Beverton–Holt equation. The Beverton–Holt model has recently been derived from an explicit resource–consumer model (Geritz and Kisdi, 2004). To see whether the results of Doebeli and Killingback (2003) hold also when quasi-local competition is mechanistically derived from underlying interactions, Kisdi and Utz (2005) extended the resource–consumer model of Geritz and Kisdi (2004) to metapopulations following the assumptions of Doebeli and Killingback (2003) and assuming a simple life history of the consumer without essential age- or stage-structure (mature adults emerge from completely inert eggs). The results of this mechanistic model contradicted those of Doebeli and Killingback (2003): No pattern formation was found in homogeneous environments.

In the present article, we show that pattern formation with quasi-local competition but without Allee-effects is in fact possible also in a mechanistic resource competition model, if we assume that the consumer population has a simple stage-structure. Here, we extend the model of Kisdi and Utz (2005) such that the consumer has a fixed, 1-year long juvenile (larval) stage before reaching maturation. The juveniles feed on the same limiting resource as the adults. Adults, but not juveniles, are mobile and forage also in adjacent patches. We show that spatial patterns form under two sets of conditions: If the adults deplete the resource and this has a large effect on juvenile survival; and in the reverse case, if the juveniles deplete the resource and this has a large effect on the adults. To our knowledge, this represents a novel mechanism of pattern formation. We do not assume any Allee-effects (directly or indirectly as, e.g., from predator saturation) for local activation. Instead, the stage-structure of the population plays a central role.

Most of the present analysis focuses on a two-patch metapopulation for simplicity. After describing the model in Section 2, we first show that the inclusion of the juvenile stage (with the consequent time delay) does not alter the stability of the equilibria as long as the juveniles do not interact with the resource (Section 3.1). Pattern formation is possible, i.e., the homogeneous equilibrium can become unstable and inhomogeneous equilibria can be stable, only when both the juveniles and the adults interact with the same resource (Section 3.2). In Section 4, we show an example of pattern formation in large metapopulations.

Section 5 contains an alternative model, which is biologically somewhat less realistic but simpler, analytically tractable, and captures the essential elements of our first model. Here, we focus on four limiting cases and show that patterned equilibria are stable under the same qualitative conditions as in the first model.

In Section 6, we show that the equation used by [Doebeli and Killingback \(2003\)](#) can be derived as a particular case of our model in Section 5. This derivation gives a mechanistic underpinning to the model of [Doebeli and Killingback \(2003\)](#) and highlights the role of stage structure in their results.

The Appendix briefly shows yet another related model with pattern formation, which is set in continuous time without seasonality. We use this model only to investigate the relationship between the present mechanism and the Turing-type diffusive instability (see Discussion).

## 2. The model

### 2.1. Assumptions

We consider a metapopulation occupying  $n$  habitat patches that lie on a circle, such that each patch has two direct neighbors and the 1st and  $n$ th habitat patches adjoin. The environment is homogeneous, i.e., the conditions in each patch are assumed to be the same.

Each habitat patch  $i$  ( $i = 1, \dots, n$ ) is inhabited by a consumer population feeding on a single resource with abundance  $R_i$ . The consumer population consists of eggs (with density  $E_i$ ), juveniles ( $y_i$ ), and adults ( $x_i$ ). Adults consume the resource in their home patch  $i$ , but spend also a fraction of their foraging time in the two neighboring patches  $i - 1$  and  $i + 1$  (quasi-local competition). The adults convert the resource into eggs, which are laid in the home patch. The eggs are completely inert during the season and hatch only at the beginning of the next year. Juveniles eat the same resource as the adults, but they do not forage in patches other than their home patch. Juveniles reach maturity after 1 year. Eggs and juveniles may die during the reproductive season as well as in winter; for simplicity, however, we assume that adult consumers die only in winter but not during the season (see [Geritz and Kisdi, 2004](#), on the consequences of relaxing this assumption).

The model has two parts, continuous-time differential equations for the within-season dynamics (1)–(4) and discrete-time equations for the between-season dynamics (5)–(8) as in [Geritz and Kisdi \(2004\)](#). Let  $m$  denote the year and  $t$  the time within a season;  $t$  runs from 0 to 1. For patches  $i = 1, \dots, n$ , the within-season dynamics is given by

$$\begin{aligned} \frac{dR_i^{(m)}(t)}{dt} = & \alpha \cdot \left[ R_i^{(m)}(t) f \left( R_i^{(m)}(t) \right) \right. \\ & \left. - \beta R_i^{(m)}(t) \left( (1-p)x_i^{(m)}(t) + \frac{p}{2} \left( x_{i-1}^{(m)}(t) + x_{i+1}^{(m)}(t) \right) \right) \right. \\ & \left. - \delta R_i^{(m)}(t) y_i^{(m)}(t) \right] \end{aligned} \tag{1}$$

$$\begin{aligned} \frac{dE_i^{(m)}(t)}{dt} = & \gamma \beta x_i^{(m)}(t) \left( (1-p)R_i^{(m)}(t) + \frac{p}{2} \left( R_{i-1}^{(m)}(t) + R_{i+1}^{(m)}(t) \right) \right) \\ & - \mu E_i^{(m)}(t) \end{aligned} \tag{2}$$

$$\frac{dy_i^{(m)}(t)}{dt} = -\eta\left(R_i^{(m)}(t)\right) y_i^{(m)}(t) \tag{3}$$

$$\frac{dx_i^{(m)}(t)}{dt} = 0. \tag{4}$$

Here,  $\alpha R_i^{(m)}(t) f(R_i^{(m)}(t))$  describes the resource dynamics in the absence of the consumer, with the function  $f$  specified later. To ease the calculations later, we have factored out  $\alpha$  in the right-hand side of Eq. (1); accordingly,  $\alpha\beta$  and  $\alpha\delta$  denote the consumption rates of adult and juvenile consumers, respectively. Since the per capita rate of consumption is  $\alpha\beta R$  and the per capita rate of egg production is  $\gamma\beta R$ ,  $\gamma/\alpha$  is the conversion factor of food into eggs. The adults spend a fraction  $p$  of their time by foraging outside their home patch. For  $n > 2$ , this time is split evenly between the two neighboring patches, such that  $(1 - p)$  of foraging time is spent in the home patch and  $p/2$  of time is spent in each of the neighboring patches. All eggs are laid in the adult’s home patch. During the season, eggs die at a constant rate  $\mu$  whereas the death rate of juveniles,  $\eta(R)$ , depends on the amount of food they consume. No adult mortality is assumed during the season.

For the between-season dynamics, we have

$$R_i^{(m+1)}(0) = \varrho R_i^{(m)}(1) \tag{5}$$

$$E_i^{(m+1)}(0) = 0 \tag{6}$$

$$y_i^{(m+1)}(0) = \sigma E_i^{(m)}(1) \tag{7}$$

$$x_i^{(m+1)}(0) = \xi y_i^{(m)}(1) + \theta x_i^{(m)}(1), \tag{8}$$

where  $\varrho$ ,  $\sigma$ ,  $\xi$ , and  $\theta$  are the overwinter survival probabilities of the resource, eggs, juveniles, and adults, respectively. Notice that unlike in [Kisdi and Utz \(2005\)](#), adults may survive and reproduce several times. For simplicity, we assume no dispersal between patches, i.e., neither juveniles nor adults change their home patch.

To complete the model, we need to specify the functions  $f(R)$  and  $\eta(R)$ . For the resource dynamics, we assume  $\alpha Rf(R) = \alpha - (\alpha R/K)$ , such that there is a constant inflow of the resource at rate  $\alpha$  into the system and an efflux at a per capita rate  $\alpha/K$ ; without consumers, the equilibrium resource level is then  $K$ . The juveniles’ death rate is assumed to decrease with increasing resources according to the positive function  $\eta(R) = \frac{a}{b+R} + c$ . Note that the death rate remains finite when there are no resources at all ( $\eta(0) = \frac{a}{b} + c$ ) and there is natural juvenile death even if plenty of resources are available ( $\lim_{R \rightarrow \infty} \eta(R) = c$ ).

Without loss of generality, we can simplify the model by scaling resource density such that  $K = 1$  and scaling consumer density such that  $\beta = 1$ . Since the density of adults remains constant within a season, we shall suppress  $t$  in connection with  $x$ .

Following [Geritz and Kisdi \(2004\)](#), we assume that the within-season dynamics of the resource is much faster than the dynamics of the consumer, i.e., we

assume that  $\alpha$  is large. Then  $R_i^{(m)}(t)$  can be approximated by its time-varying quasi-equilibrium,

$$\widehat{R}_i^{(m)}(t) = \frac{1}{1 + (1 - p)x_i^{(m)} + \frac{p}{2}(x_{i-1}^{(m)} + x_{i+1}^{(m)}) + \delta y_i^{(m)}(t)}, \tag{9}$$

which tracks the changes in juvenile density during the season. Because of the time scale separation between the resource and the consumer dynamics, the value of  $\varrho > 0$ , the overwinter survival probability of the resource, is irrelevant.

In the virgin environment,  $\widehat{R} = 1$  and the lifetime reproductive success of an adult is

$$L = \frac{1}{1 - \theta} \cdot \sigma \frac{\gamma}{\mu} (1 - e^{-\mu}) \cdot \xi e^{-\left(\frac{a}{b+1} + c\right)} \tag{10}$$

where  $\frac{1}{1-\theta}$  is the expected lifetime of an adult,  $\sigma \frac{\gamma}{\mu} (1 - e^{-\mu})$  is the number of surviving eggs per adult per season, and  $\xi e^{-\left(\frac{a}{b+1} + c\right)}$  is juvenile survival. The consumer is viable if  $L > 1$ , which we shall always assume in the subsequent analysis. Note that for  $L < 1$ , the nontrivial equilibria of the model assume negative values; when  $L = 1$ , the homogeneous equilibria undergo a transcritical bifurcation, i.e., they coincide with the trivial equilibrium.

### 2.2. Dynamics of an isolated population

Let us first briefly look at an isolated population ( $n = 1$ ) before investigating metapopulations. Assume that juvenile consumption is negligible ( $\delta = 0$ ) and juvenile mortality does not depend on the resource ( $a = 0$ ), for example, because juveniles utilize a different and nonlimiting resource. The resource then attains the constant quasi-equilibrium  $\widehat{R}^{(m)} = \frac{1}{1+x^{(m)}}$  and the within-season dynamics in Eqs. (2)–(4) can easily be integrated. For the between-season dynamics of adults, one obtains the second-order difference equation

$$x^{(m+2)} = \frac{(1 - \theta)Lx^{(m)}}{1 + x^{(m)}} + \theta x^{(m+1)}. \tag{11}$$

The model has two fixed points,  $(x^0, y^0) = (0, 0)$  and  $(x^*, y^*) = (L - 1, \frac{1-\theta}{\xi e^{-c}} x^*)$ . The trivial equilibrium  $(x^0, y^0)$  is unstable and the nontrivial equilibrium  $(x^*, y^*)$  is asymptotically stable whenever the population is viable ( $L > 1$ ). Notice that with semelparous adults ( $\theta = 0$ ), the second-order map  $x^{(m)} \mapsto x^{(m+2)}$  in Eq. (11) has the form of the [Beverton and Holt \(1957\)](#) model. Although in effect two independent populations live together (one reproduces in odd years and the other in even years), both equilibrate at the globally stable fixed point of the Beverton–Holt model. [Geritz and Kisdi \(2004\)](#) derived the Beverton–Holt dynamics for the first-order map  $x^{(m)} \mapsto x^{(m+1)}$  from a consumer–resource model similar to ours but without the juvenile stage. The presence of juveniles introduces a time delay of 1

year but does not alter the qualitative behavior of the model as long as the juveniles do not interact with the resource ( $\delta = 0$  and  $a = 0$ ). This is of importance because the first-order Beverton–Holt map formed the basis of the metapopulation models of [Doebeli and Killingback \(2003\)](#) and of [Kisdi and Utz \(2005\)](#), with whom we shall contrast the present results.

If the juveniles interact with the resource such that  $\delta > 0$  and/or  $a > 0$ , then the nontrivial fixed point cannot be found analytically and thus the model has to be investigated by numerical methods. Juveniles can destabilize the fixed point when they interact with the resource, and therefore the stage-structured population can exhibit population cycles. This happens if the juveniles consume the resource heavily but depend on it only weakly ( $\delta$  is large but  $a$  is small) and also in the converse case, i.e., if juveniles consume little but their survival strongly depends on the resource ( $\delta$  is small but  $a$  is large). In the first case, the resource is depleted and adults can hardly reproduce in years when juvenile density is large; as a consequence, there will be few juveniles in the next year but many adults, which will then produce many juveniles by the year after. In the second case, most juveniles die in years when adult density is high; there will be few adults in the next year but many juveniles, which enjoy high resource abundance and mature into many adults by the year after. These cycles are essentially the same as the single cohort dynamics found by [Bulmer \(1977\)](#) and analyzed in detail by [Davydova et al. \(2003\)](#); see Discussion). In this paper, we concentrate on stationary spatial pattern formation and thus do not pursue temporal cyclic behavior further.

### 3. Two-patch metapopulations

We analyze the model in detail for two habitat patches ( $n = 2$ ;  $i, j \in \{1, 2\}, i \neq j$ ). In this case, pattern formation amounts to the destabilization of the homogeneous equilibrium  $(x^*, y^*, x^*, y^*)$  and the stabilization of boundary equilibria where only one of the patches has a breeding population  $((\hat{x}, \hat{y}, 0, 0)$  and  $(0, 0, \hat{x}, \hat{y}))$ . Numerical simulations show that pattern formation occurs under similar conditions also in larger metapopulations (see Section 4). In this section, we first show that the homogeneous equilibrium remains stable if the juveniles do not interact with the resource, thus the mere presence of juveniles does not induce patterns. Next, we investigate pattern formation when both the juveniles and the adults interact with the same resource.

#### 3.1. Juveniles do not interact with the resource

Here, we investigate a two-patch metapopulation assuming that juvenile consumption is negligible ( $\delta = 0$ ) and juvenile survival does not depend on the amount of available resource ( $a = 0$ ). This is the case if juveniles feed on some other resource that is not limiting population growth.

This case can be solved fully analytically. The quasi-equilibrium of the resource is constant during the season ( $\widehat{R}_i^{(m)} = \frac{1}{1+(1-p)x_i^{(m)}+px_j^{(m)}}$ ) and  $\eta(R) = c$ , i.e., juveniles die at a constant rate. Integrating the within-season dynamics yields the following

equations for the between-season dynamics:

$$x_i^{(m+1)} = \xi y_i^{(m)}(0)e^{-c} + \theta x_i^{(m)} \tag{12}$$

$$y_i^{(m+1)}(0) = L \frac{1 - \theta}{\xi e^{-c}} x_i^{(m)} \tag{13}$$

$$\cdot \left( \frac{1 - p}{1 + (1 - p)x_i^{(m)} + px_j^{(m)}} + \frac{p}{1 + (1 - p)x_j^{(m)} + px_i^{(m)}} \right).$$

Besides the trivial fixed point  $(x^0, y^0, x^0, y^0) = (0, 0, 0, 0)$ , this model has a homogeneous equilibrium  $(x^*, y^*, x^*, y^*)$  where the two patches have equal population densities as well as boundary equilibria  $(\hat{x}_1, \hat{y}_1, 0, 0)$ ,  $(\hat{x}_2, \hat{y}_2, 0, 0)$ ,  $(0, 0, \hat{x}_1, \hat{y}_1)$  and  $(0, 0, \hat{x}_2, \hat{y}_2)$  where one of the two populations is extinct. The equilibrium densities are

$$x^* = L - 1 \tag{14}$$

$$y^* = \frac{1 - \theta}{\xi e^{-c}} x^* \tag{15}$$

$$\hat{x}_{1,2} = \frac{2p(1 - p)L - 1 \pm \sqrt{1 - 4p(1 - p)(1 - p(1 - p)L^2)}}{2p(1 - p)} \tag{16}$$

$$\hat{y}_i = \frac{1 - \theta}{\xi e^{-c}} \hat{x}_i \quad i = 1, 2. \tag{17}$$

Because  $\hat{x}_2$  and thus  $\hat{y}_2$  are negative, there is only one pair of biologically relevant boundary equilibria,  $(\hat{x}_1, \hat{y}_1, 0, 0)$  and  $(0, 0, \hat{x}_1, \hat{y}_1)$ .

The trivial fixed point is unstable whenever the population is viable. At the homogeneous equilibrium  $(x^*, y^*, x^*, y^*)$ , the eigenvalues of the Jacobian matrix are

$$\lambda_{1,2} = \frac{1}{2} \left( \theta \pm \sqrt{4 \left( \frac{1}{L} \right) (1 - \theta) + \theta^2} \right) \tag{18}$$

$$\lambda_{3,4} = \frac{1}{2} \left( \theta \pm \sqrt{\frac{1}{L} \left( 4 + 16p(1 - p)(L - 1)(1 - \theta) + \theta(L\theta - 4) \right)} \right). \tag{19}$$

$|\lambda_{1,2}| < 1$  for  $L > 1$ ;  $|\lambda_3| < 1$  for  $p \neq \frac{1}{2}$ ; and  $|\lambda_4| < 1$  unless both  $p = \frac{1}{2}$  and  $\theta = 0$ . The homogeneous equilibrium is thus generically stable. The eigenvalues at the boundary equilibria are too complicated to be shown here, but we have proved that the boundary equilibria are unstable for  $p \neq \frac{1}{2}$  (a *Mathematica* notebook is available on request).

In the degenerate case  $p = \frac{1}{2}$ , there is a line of equilibria given by  $\frac{x_1 + x_2}{2} = L - 1$  and  $y_i = \frac{1 - \theta}{\xi e^{-c}} x_i$  ( $i = 1, 2$ ), which includes the homogeneous equilibrium and the boundary equilibria of the generic case. This line is attracting, but points on the

line are neutral. When the adults split their time evenly between the two patches and the juveniles do not consume, the resource is depleted evenly and the total population size equilibrates irrespective of where the adults lay their eggs. If  $\theta = 0$  in addition to  $p = \frac{1}{2}$ , the model shows neutral out-of-phase cycles. With semelparous adults, there are two independent metapopulations (reproducing, respectively, in odd and in even years), which equilibrate on the neutral line but usually at different points. Consequently, the total number of adults and the total number of juveniles are constant over time but the distribution of individuals over the patches oscillates in a 2-year cycle. Recall that with semelparous adults but  $p \neq \frac{1}{2}$ , the metapopulations reproducing in odd and in even years both equilibrate to the stable homogeneous fixed point.

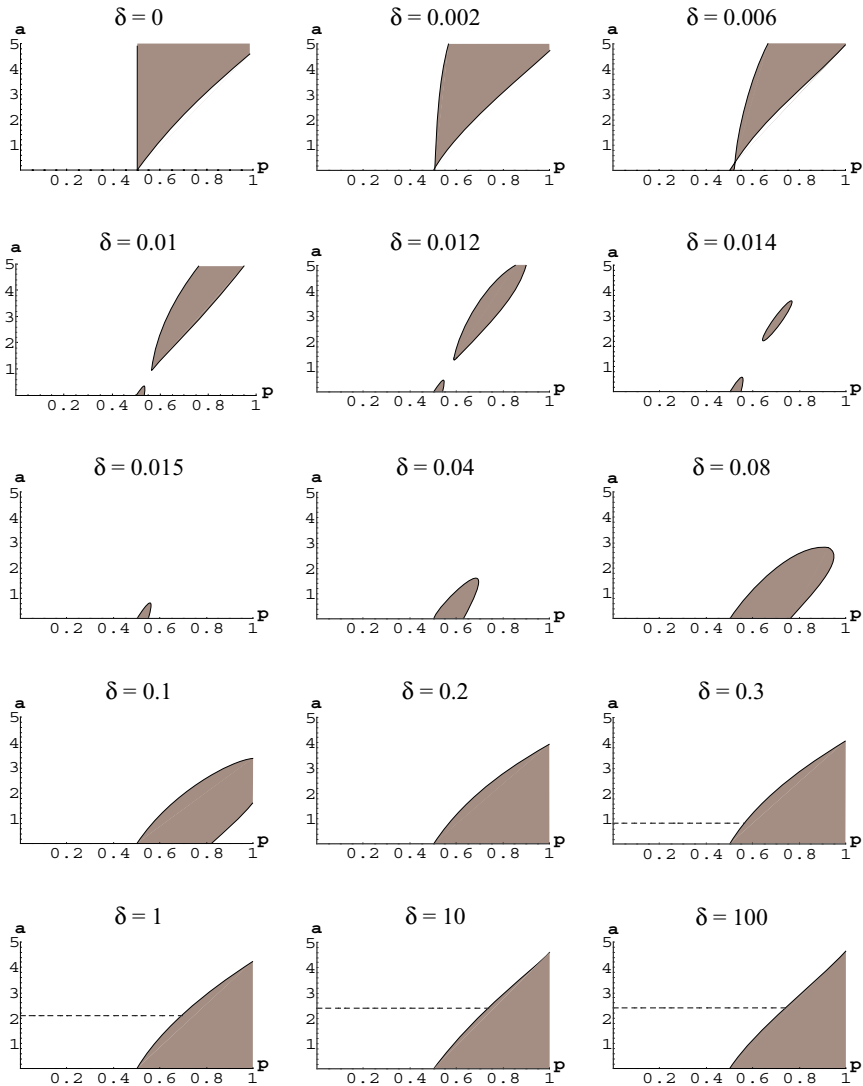
We conclude that if the juveniles do not affect the resource level and the resource does not affect juvenile survival, then generically the homogeneous equilibrium is the only stable equilibrium. The model of [Kisdi and Utz \(2005\)](#), which did not include the juvenile stage, gives the same result (except the neutral cycles of a highly degenerate case); even the equilibrium densities of adults are the same in the two models. As in the case of a single isolated population (Section 2.2), the time delay caused by the juvenile stage does not alter the behavior of the model per se.

### 3.2. Juveniles interact with the resource

Let us now consider the full model where juveniles consume a nonnegligible amount of the resource ( $\delta > 0$ ) and their survival depends on resource abundance ( $a > 0$ ). With  $a > 0$ , the fixed point of the between-season dynamics cannot be given explicitly; and with  $\delta > 0$ , we cannot solve the differential equations for the eggs and juveniles analytically. Therefore we investigated the model numerically using the software package *Mathematica* (Wolfram Research). As we concentrate on the role of juveniles in spatial pattern formation, we use  $\delta$ ,  $a$ , and  $p$  as bifurcation parameters and fix the values of  $b$ ,  $c$ ,  $\mu$ ,  $\sigma$ ,  $\xi$ ,  $\theta$ , and  $L$ . The latter determines the value of  $\gamma$ ; notice that as we vary  $a$ , we also vary  $\gamma$  such that  $L > 1$  stays constant and the population remains viable.

In the numerical procedure, we choose a value for  $\delta$  and start with locating an approximate equilibrium for  $a = 0$  and  $p = 0$  by simulation. This approximate result is used to obtain the precise equilibrium densities by numerically integrating the within-season dynamics and finding the root of the between-season difference equations. To establish the stability of the equilibrium, we differentiate the between-season equations numerically and calculate the eigenvalues of the Jacobian matrix. Next, we change the values of  $p$  and  $a$  incrementally and use a continuation technique to find the equilibria and their stability.

The results of the numerical analysis are shown in Fig. 1. Stationary pattern formation occurs in the shaded areas of the parameter space. In these areas, the homogeneous equilibrium  $(x^*, y^*, x^*, y^*)$  is unstable and two inhomogeneous (boundary) equilibria,  $(\hat{x}, \hat{y}, 0, 0)$  and  $(0, 0, \hat{x}, \hat{y})$ , are locally asymptotically stable. As before, one of the two patches is empty at the inhomogeneous equilibrium in the sense that no adult lays eggs here and there are no juveniles, but both patches contain foraging adults. The dynamics of a metapopulation where only one patch



**Fig. 1** Stationary pattern formation in two-patch metapopulations. Stable patterns exist, i.e., the inhomogeneous equilibria are locally asymptotically stable inside the *shaded* areas. In the parameter range shown, the homogeneous equilibrium is stable outside the *shaded* areas but for large values of  $\delta$ , only above the *dotted* line. The inhomogeneous equilibria are unstable outside the *shaded* areas. Other parameter values are  $b = c = 1$ ,  $\mu = \sigma = \xi = \theta = 0.2$ ,  $L = 5.5$ .

has a breeding population is thus different from a single isolated population unless  $p = 0$ . Outside the shaded areas, the boundary equilibria are unstable, but the homogeneous equilibrium is not stable everywhere.

Next to the homogeneous and inhomogeneous equilibria, the model has also cyclic attractors. When an isolated patch exhibits cyclic dynamics (see Section 2.2),

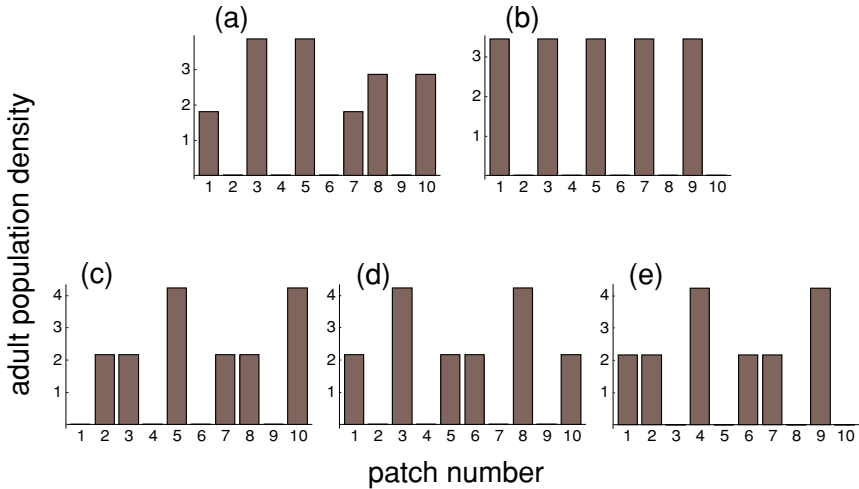
then the two-patch metapopulation must have both in-phase and out-of-phase cycles for  $p = 0$  and, by continuity, also for sufficiently small values of  $p$ . There is a part of the parameter space where neither the homogeneous nor the inhomogeneous equilibria are stable; all orbits must then converge to some nonequilibrium attractor (within the parameter range shown in Fig. 1, this occurs for large values of  $\delta$  below the dotted lines). Moreover, for some parameters, a cyclic attractor exists simultaneously with the locally stable inhomogeneous equilibria such that it depends on the initial population densities whether the metapopulation converges to a stationary pattern or exhibits sustained oscillations. In the remainder of this article, however, we focus on stationary patterns only.

In Fig. 1, there exist two distinct areas where stationary patterns are stable: There is an upper region that shrinks with increasing  $\delta$  and disappears at about  $\delta = 0.015$  and there is a lower region that increases as  $\delta$  increases. These two areas correspond to two different mechanisms of pattern formation. For a heuristic interpretation, assume that the first patch is occupied by a large population but the second patch contains only a small population. Consider first the upper region, i.e., assume that  $\delta$  is small but  $a$  is large: Juveniles consume only a small amount of the resource, but this consumption is nevertheless important for their survival. When  $p$  is sufficiently large, adults from the first patch deplete the resource in the second patch. Juveniles in the second patch have high mortality, thus the small population of the second patch declines further and the metapopulation attains an inhomogeneous (boundary) equilibrium.

Consider now the situation when  $\delta$  is large and  $a$  is small, as in the lower regions of pattern formation in Fig. 1. In this case, juveniles consume the resource more heavily than adults, but juveniles suffer less when the resource is in short supply (e.g., they can switch to an alternative resource when necessary). This situation is thus the reverse of the previous one. When there are many juveniles in the first patch, they deplete the local resource, but this does not harm them and, assuming that  $p$  is large, does not harm the adults of the first patch since they mainly forage in the second patch. The adults of the second patch, however, find little food when they forage in the first patch. A small population in the second patch thus will decline and the inhomogeneous equilibrium is stable. For intermediate values of  $\delta$ , both mechanisms are at work; when  $\delta$  increases, the first mechanism weakens and hence the upper region decreases, whereas the second mechanism becomes stronger and the lower region grows.

In a two-patch metapopulation, both mechanisms work only if  $p$  exceeds  $\frac{1}{2}$ , i.e., if adults spend more time in the other patch than in their home patch. This may in fact be adaptive (to decrease competition with the immobile juveniles), but may nevertheless look less realistic for many biological systems. In larger metapopulations, however,  $p$  exceeds  $\frac{1}{2}$  if, e.g., adults split their foraging time evenly among the three patches they can reach, i.e., the home patch and the two neighboring patches.

In the model of Doebeli and Killingback (2003), pattern formation occurs whenever  $p$  exceeds  $\frac{1}{2}$ . In our model, the inhomogeneous equilibria are stable for all  $p > \frac{1}{2}$  only if either  $\delta = 0$  and  $a$  is sufficiently large or  $\delta$  is large and  $a = 0$  (Fig. 1). These two cases thus qualitatively correspond to the model of Doebeli and Killingback (2003; see also Sections 5 and 6 later). In both models, the



**Fig. 2** Different stationary attractors of a 10-patch metapopulation. The bars show the density of adults that reproduce in a given patch,  $x_i$ . Parameter values are  $\delta = 0.1$ ,  $a = 1$ ,  $p = 0.8$ ,  $b = c = 1$ ,  $\mu = \sigma = \xi = \theta = 0.2$ ,  $L = 5.5$ .

homogeneous equilibrium can be destabilized only if the adults spend more than half of their foraging time outside their home patch.

#### 4. Large metapopulations

We investigated pattern formation in a larger metapopulation ( $n = 10$ ) relying on simulations only. In Fig. 2, the parameters are chosen such that a two-patch metapopulation would exhibit a stable pattern. The 10-patch model may converge to a number of inhomogeneous equilibria for the same parameter values, depending on the initial values of  $x_i^{(1)}$  and  $y_i^{(1)}(0)$  ( $i = 1, \dots, 10$ ). Some of these equilibria are simply shifted along the row of patches (see the panels (c)–(e) of Fig. 2). The groups of shifted equilibria are analogous to the pairs of boundary equilibria in the two-patch model. Although shifts are mathematically trivial, for the population in a certain patch it makes a big difference on which attractor the metapopulation settles. Other equilibria are qualitatively different (panels (a) and (b) of Fig. 2), with different arrangement and population size of patches occupied by breeding populations (recall that empty patches also contain foraging adults). The existence of multiple stationary attractors is very similar to the results of [Doebeli and Killingback \(2003\)](#).

#### 5. An alternative model

The model we investigated earlier is a natural extension of [Geritz and Kisdi \(2004\)](#) and [Kisdi and Utz \(2005\)](#) to populations with separate juvenile and adult stages.

This extension had to be analyzed numerically, because (for  $\delta > 0$ ) the within-season dynamics could not be integrated explicitly.

In this section, we consider an alternative model where we can obtain limiting results analytically. Moreover, in this alternative model, we do not need to assume particular functions for the resource dynamics ( $f(R)$ ) and for the juvenile death rate ( $\eta(R)$ ): The results of this section hold for arbitrary decreasing functions (see later).

To achieve such general results, we need to assume that within each season, the number of juveniles attains an equilibrium. Biologically, this assumption may be less realistic: it implies that not only the resource but also juvenile density changes fast on a time scale where adult density is assumed constant. Mathematically, however, this assumption eliminates the need for integrating the within-season dynamics and thereby greatly simplifies the analysis.

We further simplify the model by eliminating the inert egg stage. In this model, we shall thus assume that adults produce juveniles throughout the season depending on how much resources they consume; juveniles die at rate  $\eta(R)$  whereas adult density stays constant. The dynamics within a season is given by

$$\frac{dR_i(t)}{dt} = R_i(t) f(R_i(t)) - \beta R_i(t) [(1 - p)x_i + (p/2)(x_{i-1} + x_{i+1})] - \delta R_i(t) y_i(t) \tag{20}$$

$$\frac{dy_i(t)}{dt} = x_i \phi((1 - p)R_i(t) + (p/2)(R_{i-1}(t) + R_{i+1}(t))) - \eta(R_i(t)) y_i(t) \tag{21}$$

$$\frac{dx_i(t)}{dt} = 0. \tag{22}$$

Here,  $\phi(R)$  is the number of juveniles produced by an adult who consumed  $\beta R \cdot dt$  resources in time  $dt$ . Birth rate may be proportional to the amount of resource consumed ( $\phi(R) = \gamma\beta R$  as in our first model) but this is not necessary: We assume only that  $\phi(R)$  is an increasing function. The resource dynamics need not be specified, but we assume that  $f(R)$  is strictly decreasing (no Allee-effects) and that resource density is scaled such that its carrying capacity is 1 ( $f(1) = 0$ ). The death rate of juveniles,  $\eta(R)$ , is either constant or an arbitrary decreasing function of resource density that assumes nonnegative values.

The within-season dynamics in Eqs. (20)–(22) is run to equilibrium. At the beginning of the next season, we have

$$R_i^{(m+1)}(0) = \varrho \bar{R}_i^{(m)} \tag{23}$$

$$y_i^{(m+1)}(0) = 0 \tag{24}$$

$$x_i^{(m+1)} = \xi \bar{y}_i^{(m)} + \theta x_i^{(m)}, \tag{25}$$

where bars denote the equilibrium densities obtained from Eqs. (20)–(22); note that the value of  $\varrho > 0$  is irrelevant due to the assumption of within-season equilibrium.

In this section, we consider only two patches and only the local stability of stationary patterns. Therefore, we investigate the local stability of the inhomogeneous equilibrium  $(\hat{x}_1, 0)$  against the invasion of a population breeding in patch 2, assuming that the equilibrium is stable with respect to perturbations of  $x_1$ . Note, however, that the latter condition does not always hold: The model can exhibit cyclic behavior in the discrete between-year dynamics.

We now consider four limiting cases of the model, which differ whether the juveniles or the adults deplete the resource and whether the juveniles or the adults depend on the resource. In comparison to our first model (Fig. 1), these four cases correspond, respectively, to (1)  $\delta = 0$ , large  $a$ ; (2) large  $\delta$ ,  $a = 0$ ; (3)  $\delta = 0$ ,  $a = 0$ ; and (4) large  $\delta$ , large  $a$ .

*Case 1. Only the adults deplete the resource but only the juveniles depend on it*

Assume that juvenile consumption is negligible ( $\delta = 0$ ) but juvenile mortality nevertheless depends on the little food juveniles consume ( $\eta(R)$  is strictly decreasing). Adults consume the resource ( $\beta > 0$ ) but their reproduction does not depend on it ( $\phi(R) \equiv k$  is constant); this is possible if the adults can use also an alternative resource for reproduction when necessary. If patch 2 has no breeding population, then the within-season equilibrium of Eqs. (20)–(22) simplifies to  $f(\bar{R}_1) = \beta(1 - p)x_1$ ,  $f(\bar{R}_2) = \beta px_1$  and  $\bar{y}_1 = kx_1/\eta(\bar{R}_1)$ . The between-season dynamics of adults is thus given by

$$x_1^{(m+1)} = \left[ \frac{\xi k}{\eta(f^{-1}(\beta(1 - p)x_1^{(m)}))} + \theta \right] x_1^{(m)} \tag{26}$$

and the fixed point  $\hat{x}_1$  can be determined by setting the expression between the brackets equal to 1.

Analogously, the between-year dynamics of a small population introduced into patch 2 when the population in patch 1 has reached  $\hat{x}_1$  is  $x_2^{(m+1)} = \left[ \frac{\xi k}{\eta(f^{-1}(\beta p \hat{x}_1))} + \theta \right] x_2^{(m)}$ . This population dies out if and only if

$$\frac{\xi k}{\eta(f^{-1}(\beta p \hat{x}_1))} + \theta < 1 = \frac{\xi k}{\eta(f^{-1}(\beta(1 - p)\hat{x}_1))} + \theta. \tag{27}$$

Because  $f(R)$  and  $\eta(R)$  are strictly decreasing, this condition is equivalent to  $p > 0.5$ . The pattern  $(\hat{x}_1, 0)$  is thus stable against a perturbation of  $x_2$  whenever  $p$  is greater than a half. (Recall that in larger metapopulations,  $p > 0.5$  is achieved,

e.g., if the adults split their foraging time equally between the home patch and its two neighboring patches.)

*Case 2. Only the juveniles deplete the resource but only the adults depend on it*

This is the opposite case: Here we assume that juveniles consume the resource ( $\delta > 0$ ) although their survival does not depend on their consumption ( $\eta(R) \equiv h$  is constant). The consumption of adults is negligible ( $\beta = 0$ ), yet their reproduction depends on the very small amount they eat of this resource ( $\phi(R)$  is strictly increasing).

When patch 2 has no breeding population, then it has no juveniles and therefore  $\bar{R}_2 = 1$ . In patch 1, the equilibrium density of juveniles is  $\bar{y}_1 = x_1 \phi((1 - p)\bar{R}_1 + p) / h$ , and the between-season dynamics of adults is given by

$$x_1^{(m+1)} = \left[ (\xi/h)\phi((1 - p)\bar{R}_1 + p) + \theta \right] x_1^{(m)}. \tag{28}$$

A small population in patch 2, introduced when the population in patch 1 has attained its fixed point  $\hat{x}_1$ , is exponentially declining if and only if

$$(\xi/h)\phi(p\bar{R}_1 + (1 - p)) + \theta < 1 = (\xi/h)\phi((1 - p)\bar{R}_1 + p) + \theta. \tag{29}$$

Since  $\bar{R}_1 < 1$  at the inhomogeneous equilibrium  $(\hat{x}_1, 0)$  and  $\phi(R)$  is increasing, the condition mentioned earlier is equivalent to  $p > 0.5$ . Just as in the previous case, the pattern is stable whenever  $p$  exceeds 0.5.

*Case 3. Juveniles do not interact with the resource*

Now we assume that juveniles neither consume the resource ( $\delta = 0$ ) nor depend on it ( $\eta(R) \equiv h$  is constant), whereas adults deplete the resource ( $\beta > 0$ ) and their reproduction is affected ( $\phi(R)$  is strictly increasing). When patch 2 has no breeding population, we have  $f(\bar{R}_1) = \beta(1 - p)x_1$ ,  $f(\bar{R}_2) = \beta p x_1$  and  $\bar{y}_1 = x_1 \phi((1 - p)\bar{R}_1 + p\bar{R}_2) / h$  in the within-season equilibrium. The between-season dynamics of adults is then

$$x_1^{(m+1)} = \left[ (\xi/h)\phi\left((1 - p)f^{-1}(\beta(1 - p)x_1^{(m)}) + pf^{-1}(\beta p x_1^{(m)})\right) + \theta \right] x_1^{(m)}. \tag{30}$$

A small population introduced in patch 2 cannot invade if and only if

$$\begin{aligned} & (\xi/h)\phi\left((1 - p)f^{-1}(\beta p x_1^{(m)}) + pf^{-1}(\beta(1 - p)x_1^{(m)})\right) + \theta \\ & < 1 = (\xi/h)\phi\left((1 - p)f^{-1}(\beta(1 - p)\hat{x}_1) + pf^{-1}(\beta p \hat{x}_1)\right) + \theta \end{aligned} \tag{31}$$

Because  $\phi(R)$  is increasing, this condition is equivalent to

$$(1 - 2p)f^{-1}(\beta p \hat{x}_1) < (1 - 2p)f^{-1}(\beta(1 - p)\hat{x}_1), \tag{32}$$

where  $f^{-1}$  is decreasing. If  $p < 0.5$ , this condition simplifies to  $p > 1 - p$ , which is impossible. If  $p > 0.5$ , then the condition reduces to  $p < 1 - p$ , which is also contradictory. The pattern  $(\hat{x}_1, 0)$  is therefore not stable against an invading population in patch 2 ( $p = 0.5$  is neutral). The case of inactive juveniles is similar to the model of [Kisdi and Utz \(2005\)](#) and Section 3.1 earlier, except for the assumption of within-season equilibrium. In agreement with the previous models, the pattern is not asymptotically stable for any value of  $p$  and neutrally stable for  $p = 0.5$ .

*Case 4. Adults do not interact with the resource*

If juveniles consume the resource ( $\delta > 0$ ) and depend on it ( $\eta(R)$  is strictly decreasing) but adults consume only an alternative and nonlimiting resource such that  $\beta = 0$  and  $\phi(R) \equiv k$  is constant, then the within-season dynamics simplifies to

$$\frac{dR_i(t)}{dt} = R_i(t)f(R_i(t)) - \delta R_i(t)y_i(t) \tag{33}$$

$$\frac{dy_i(t)}{dt} = kx_i - \eta(R_i(t))y_i(t). \tag{34}$$

Quasi-local competition ( $p$ ) plays no role in this case. Each patch equilibrates independently of the other, and an empty patch can always be invaded: No pattern is stable.

**6. Mechanistic underpinning to the model of [Doebeli and Killingback \(2003\)](#)**

[Doebeli and Killingback \(2003\)](#) investigated quasi-local competition using the model

$$x_i^{(m+1)} = \frac{\lambda x_i^{(m)}}{1 + A \left[ (1 - p)x_i^{(m)} + \frac{p}{2} (x_{i-1}^{(m)} + x_{i+1}^{(m)}) \right]} \tag{35}$$

(cf. their Eq. (8)). This model can be derived as a special case of our model in Section 5 as follows. Let  $f(R) = \alpha(1 - R/K)$ ,  $\eta(R) = a - bR$ , and let  $\phi(R) = k$  constant,  $\delta = 0$  and  $\theta = 0$  in Eqs. (20)–(22) and Eqs. (23)–(25). These assumptions correspond to Case 1 of the previous section with a logistically growing resource and a linear relationship between resource abundance and juvenile death rate. Because  $\eta(R)$ , the death rate of juveniles, should not become negative in the range of interest, assume further that  $a - bK \geq 0$ . Under these assumptions, Eqs. (20)–(22) yield

$$\bar{y}_i^{(m)} = \frac{kx_i^{(m)}}{a - bK + \frac{\beta bK}{\alpha} \left[ (1 - p)x_i^{(m)} + \frac{p}{2} (x_{i-1}^{(m)} + x_{i+1}^{(m)}) \right]} \tag{36}$$

for the within-season equilibrium of juveniles. With semelparous adults ( $\theta = 0$ ), the between-year dynamics of adults is simply  $x_i^{(m+1)} = \xi \bar{y}_i^{(m)}$  and therefore has the form of the Doebeli–Killingback equation in Eq. (35) with parameters  $\lambda = \frac{\xi k}{a-bK}$  and  $A = \frac{\beta b K}{\alpha(a-bK)}$ .

## 7. Discussion

We investigated pattern formation under quasi-local competition in a metapopulation where local populations have a simple stage-structure: We assumed that a fixed-length juvenile period precedes maturation and only adults exert competition outside their home patch. In our main model (Sections 2–4), we found that the homogeneous equilibrium can be destabilized and inhomogeneous (boundary) equilibria can be locally stable in a metapopulation with quasi-local competition under two sets of conditions: either

- (1) mainly the adults deplete the limiting resource and the shortage of resource harms mainly the juveniles

or

- (2) mainly the juveniles deplete the limiting resource and the shortage of resource harms mainly the adults.

In the first case, the adult stage is the “critical” stage (Charlesworth, 1980) that has the largest impact on the limiting resource whereas the juvenile stage is the most “sensitive” stage. In the second case, the roles are reversed. At a first glance, it may seem counterintuitive that impact and sensitivity can differ, for example that individuals may consume a resource and yet not be much harmed when the resource is in short supply. This can however be the case when there is another, substitutable resource available. It is also possible that consumption is small, yet this little amount is essential. The potential difference between impact and sensitivity has profound implications on species coexistence (Leibold, 1995; Meszéna et al., 2006) and on the dynamics of single populations with stage-structure (Davydova et al., 2003; see later). We find that the same difference is essential also in pattern formation under quasi-local competition in metapopulations.

The results of our main model (Sections 2–4) are corroborated by a simpler alternative model described in Section 5. A considerable advantage of the analysis in Section 5 is that we did not have to commit ourselves to specific functions to describe resource dynamics and the resource-dependent mortality rate of juveniles.

In both models, we assumed that for adults, the amount of available resource affects fecundity but not survival. Adult mortality was assumed to occur between, but not during, the reproductive seasons. Relaxing these simplifying assumptions could lead to much more complicated dynamics even in a single, isolated population (Wikan and Mjølhus, 1995; Geritz and Kisdi, 2004); we wanted to avoid this complication in order to focus on stationary patterns. As a further simplification, we assumed no dispersal between the patches, in the sense that offspring have always the same home patch as their parents. Passive dispersal would likely hinder

pattern formation (as in the models of [Doebeli and Killingback, 2003](#); [Kisdi and Utz, 2005](#); see, however, [Hastings, 1992](#)).

In [Fig. 1](#), we performed a bifurcation analysis of equilibria in our main model with respect to three key parameters,  $p$  (the fraction of time adults spend foraging outside their home patch),  $a$  (how strongly juvenile survival depends on the resource), and  $\delta$  (how much juveniles deplete the resource). Unfortunately, the model has seven more parameters ( $b$ ,  $c$ ,  $\mu$ ,  $\sigma$ ,  $\xi$ ,  $\theta$ , and  $\gamma$ ; the latter we varied simultaneously with  $a$  such that  $L$ , the lifetime reproductive success in a virgin environment, stays constant and greater than 1 in order to ensure viability). A full bifurcation analysis of the model would therefore be prohibitively demanding. By continuity, however, we know that small changes in the fixed parameters of [Fig. 1](#) will not lead to qualitative differences in the bifurcation diagrams. Similarly, introducing small dispersal between the patches will not destroy the patterns. In contrast to the model of [Kisdi and Utz \(2005\)](#), here we find robust patterns that do not depend on fine-tuning the model parameters.

Pattern formation includes the destabilization of the homogeneous equilibrium as well as the stabilization of patterns. In [Fig. 1](#), the homogeneous equilibrium is always unstable when the inhomogeneous equilibria are stable (i.e., in the shaded areas). It does not follow, however, that every perturbation of the homogeneous equilibrium is attracted to a patterned equilibrium, because the system can also exhibit cyclic dynamics. Indeed, we found that an in-phase cycle can be stable also simultaneously with the inhomogeneous equilibria (data not shown).

Pattern formation found in the model of [Doebeli and Killingback \(2003\)](#) corresponds to the stable patterns we find in Case 1 of our alternative model in section 5, and is similar to pattern formation in our main model with  $\delta = 0$  and large  $a$ . While our results are close to those of [Doebeli and Killingback \(2003\)](#), we could find a mechanistic underpinning to that model only by assuming stage-structured populations where different stage classes compete for the same resource with different impacts and sensitivities. In Section 6, we derived the model of [Doebeli and Killingback \(2003\)](#) explicitly from our simplified model in Section 5, assuming that adults deplete a resource that is important for juvenile survival and using a particular choice of functions for the resource dynamics and for the death rate of juveniles. As shown by this derivation as well as by the negative results of [Kisdi and Utz \(2005\)](#) and Section 3.1, the stage-structure is essential for pattern formation. For a heuristic explanation of this fact, notice that the model of [Doebeli and Killingback \(2003](#); see Eq. (35) earlier) assumes that individuals of a focal patch exert competitive influence on the neighboring patches without being affected by competition experienced outside the home patch (the denominator of Eq. (35) contains competition in the focal patch only; see [Kisdi and Utz, 2005](#)). Exerting competition while not being affected by competition is hard to realize in an unstructured population where all individuals are alike, but possible to obtain, as a limiting case, when the population is structured such that different individuals have different impacts and sensitivities. In the present case, mobile adults exert competition in the neighboring patches but they are not sensitive to competition.

An important common conclusion of [Doebeli and Killingback \(2003\)](#) and the present study is that in large metapopulations (Section 4, [Fig. 2](#)), a large number of locally stable equilibria exist for the same set of parameter values. An important

difference is, however, that our main model (Sections 2–4) often exhibits cyclic dynamics, and cycles may occur also in the alternative model of Section 5 with certain choices of functions. This is not the case in the model of [Doebeli and Killingback \(2003\)](#). By continuity, cycles will not occur in our alternative model if functions are chosen to be sufficiently similar to those assumed in Section 6 to derive the equation used by [Doebeli and Killingback \(2003\)](#).

### *7.1. Alternative mechanisms of pattern formation*

The best-known mechanism of pattern formation is diffusive instability ([Turing, 1952](#)). For stationary patterns to form in a reaction–diffusion system, there must be (at least) two interacting chemicals, species, etc., with the following three properties ([Segel and Jackson, 1972](#); see, e.g., [Edelstein-Keshet, 1988](#), for review): (i) diffusion rates must be different, (ii) all interactions between the participants (including, e.g., competition and reproduction) are local, and (iii) without diffusion, when the dynamics are given by an ODE system, the Jacobian must have one of two possible sign structures, namely either one row or one column of the Jacobian must contain positive elements and the other row or column must contain negative elements.

In our models, there are two different active stages and they have contrasting mobility as only adults forage outside their home patch; this is similar to (i). There is however an important difference between quasi-local competition and diffusion regarding (ii): We assume that adults foraging outside the home patch deplete the resource of adjacent patches, but produce offspring in the home patch. These adults thus have a negative effect on the adjacent patches via competition and, at the same time, a positive effect on the home patch via reproduction. In contrast, reaction–diffusion models assume that individuals affect the population only at one place at a time.

Because quasi-local competition violates property (ii) seen earlier, the dynamics in a single isolated patch need not conform with the two possibilities in (iii). In the Appendix, we briefly describe a model closely related to the ones analyzed in the main text, but set in continuous time. This facilitates the comparison with the continuous-time models of diffusive instability. We indeed find that in our model, the sign structure of the Jacobian is different from the two types that are possible with diffusive instability.

Due to the assumption of fast resource dynamics, the present model is in essence a single-species model; the densities of juveniles and adults at time  $t$  unequivocally determine the quasi-equilibrium resource abundance and hence juvenile mortality and adult fecundity at  $t$ . Pattern formation is known to occur in a single species if quasi-local competition operates together with local Allee-effects ([Gyllenberg et al., 1999](#)) or, in continuous space, if the characteristic range of competition is larger than that of an Allee-effect ([Levin and Segel, 1985](#); see also [Britton, 1989](#); [Furter and Grinfeld, 1989](#)). In both cases, competition provides lateral inhibition and the Allee-effects ensure local activation, which together lead to patterns. There is lateral inhibition also in our models (either the adults suppress juveniles in the adjacent patches or juveniles of the focal patch suppress reproduction of those adults

which arrive to forage from the neighboring patches). However, we do not have any Allee-effect: In a single patch, population growth is in no way enhanced by increased density of either juveniles or adults. Local activation could be substituted by locally favorable conditions when the environment is slightly heterogeneous (Gurney and Nisbet, 1976; Sasaki, 1997; Kisdi and Utz, 2005), but we assume a perfectly homogeneous environment.

Hastings (1992) found that age-dependent dispersal can destabilize the homogeneous equilibrium in age-structured metapopulations. In his two-age class model, Hastings (1992) assumed that juveniles are nondispersing whereas adults are fully mixed. The homogeneous equilibrium can then be destabilized in two different ways: Either an eigenvalue becomes less than  $-1$  and cyclic/chaotic dynamics appear (even if the corresponding single-patch system is stable), or the same eigenvalue exceeds 1, suggesting the formation of stationary patterns. It may not be immediately obvious from Hastings' (1992) paper (which focuses on the first possibility), but the latter case can occur only in the presence of Allee-effects. (To see this, calculate the left-hand side of Hastings' inequality (12) explicitly. Even if juveniles reproduce, their fecundity cannot exceed 1 in equilibrium; hence the inequality can be satisfied only if the per capita fecundity of juveniles or that of adults increases with the density of juveniles at the equilibrium of a single patch.) In contrast to Hastings' (1992) model, we obtain pattern formation without assuming Allee-effects.

Quasi-local competition amounts to some release from competition in the home patch, and this facilitates local population growth. Passive diffusion has a similar effect as it removes competitors from densely populated areas, yet diffusion does not lead to pattern formation in single-species models. As discussed earlier, the key difference is whether adults foraging elsewhere still reproduce in their home patch. Quasi-local competition releases local competition but retains reproduction.

In our models, quasi-local competition leads to pattern formation only if the two stage classes have opposite impacts and sensitivities toward the common resource (cf. the two sets of conditions described at the beginning of the Discussion). In competition between species, analogous conditions lead to mutual competitive exclusion. Indeed, pattern formation in our two-patch models can be explained as competitive exclusion of one population by the other as follows (cf. Section 3.2; see also Doebeli and Killingback, 2003). Assume that adults deplete the resource and juveniles are sensitive to the shortage of resource (case (1) mentioned earlier). When  $p$  is large enough, the adults of the first population deplete mainly the resource in the second patch, on which resource the growth of the second population mostly depends. At the same time, adults of the first population do not consume much resource in the first patch, i.e., they do not harm their own juveniles. Competition between the two populations is thus stronger than competition within a population, which implies competitive exclusion. The other possibility is that juveniles deplete the resource and adults are sensitive to it (case (2) mentioned earlier). Then, the juveniles of the first population deplete the resource at the place where the adults of the second population come to forage; at the same time, the adults of the first population are not harmed by their own juveniles because they forage in the second patch. Again, between-population competition is stronger.

Levin (1974) described a simple way of pattern formation based on competitive exclusion. Assume that two species can mutually exclude one another, i.e., a single population can have either species 1 or species 2 in a stable equilibrium. If two patches are uncoupled, they can contain different species, resulting in patterns in both species' abundances. By continuity, the pattern remains stable also for moderate values of dispersal.

Although both Levin's (1974) and our mechanisms are based on competitive exclusion, note the following differences. In our case, competitive exclusion occurs between the populations that reproduce in the two patches, not between two species within the same patch. Accordingly, our mechanism does not require that a single population has multiple stable equilibria. In Levin's model, the two homogeneous equilibria (where both patches are occupied by the same species) are always stable, whereas in our model, the (unique) homogeneous equilibrium is not always stable. The mobility of adults is essential in our case to obtain quasi-local competition, whereas in Levin's model mobility amounts to passive dispersal and the pattern is most robust if the individuals are immobile.

When an isolated patch exhibits complex population dynamics, dispersal can lead to pattern formation in the form of spatiotemporal chaos, in which spatial patterns exhibit complicated temporal dynamics (Kaneko, 1998). However, even with complex single-patch dynamics, dispersal between patches may also stabilize the dynamics and may lead to oscillating or even static patterns in space (e.g., the "crystal lattice" pattern obtained by Hassell et al., 1991; see also Hastings, 1993; Gyllenberg et al., 1993; Doebeli, 1995; Lloyd, 1995; Doebeli and Ruxton, 1998; Kaneko, 1998). The formation of static patterns through dispersal can also be interpreted as competitive exclusion (Doebeli and Ruxton, 1998). Assume that before dispersal, there is high population density in the first patch and low density in the second. If most individuals disperse, then densities after dispersal are reversed. Under strong density dependence, the few individuals left in the first patch can produce many offspring whereas the population of the second patch crashes, which restores the original pattern of densities a full generation later. By sending many dispersers, the first population keeps the second patch at low density or excludes the second population altogether. This mechanism of pattern formation works only if large populations crash (overcompensation), which is not necessary in our models. For example, the model of Doebeli and Killingback (2003), which we derive as a special case in Section 6, never exhibits cycles and its single-patch version is the well known undercompensating Beverton and Holt (1957) model.

## 7.2. Pattern formation and single-cohort cycles

Opposite impacts and sensitivities of the stage classes are strikingly similar to the conditions under which a structured population exhibits single-cohort cycles (Bulmer, 1977; Davydova et al., 2003). Indeed, we also find cyclic dynamics already in a single isolated patch, and under qualitatively the same conditions as pattern formation in metapopulations (see Section 2.2).

In the case of semelparous adults ( $\theta = 0$ ), the organism in our main model (Sections 2–4) is a strictly biennial species and the population consists of two

isolated cohorts reproducing in even and odd years, respectively. Cycles result from competitive exclusion of one cohort by the other (Bulmer, 1977), such that in even (odd) years there are only juveniles (adults) or *vice versa*. Analyzing strict biennials, Davydova et al. (2003) found that the single-cohort dynamics is stable if one age class has higher (expected) competitive impact but the other age class is more sensitive to it. In this case, either cohort can competitively suppress the other because their high-impact age class is present when the other cohort has the high-sensitivity class. (Davydova et al. (2003) assumed a Ricker-type density dependence instead of explicit resource competition; because this allows for complex dynamics, they have the result mentioned earlier only for moderate fecundities.)

We emphasize the common structure of mutual competitive exclusion between different patches and between different cohorts of biennials. In both cases, the high-impact stage has the opportunity to suppress the competitor's high-sensitivity stage. Under quasi-local competition, adults of one population live (mainly) together with the juveniles of the other population; during the single-cohort cycles of biennials, adults of one cohort live together with juveniles of the other cohort. When different stage classes of the competitors live together, mutual exclusion results if one class has high impact and the other class has high sensitivity.

Single-cohort cycles can also occur in longer-lived semelparous populations, such as periodical cicadas. These cycles require that one cohort can exclude all other cohorts, i.e., if the competitive effect on itself, averaged over the lifetime, is smaller than on any other cohort (Bulmer, 1977). The single-cohort dynamics of longer-lived species is analogous to a larger metapopulation where only one patch contains a breeding population. By analogy to the single-cohort case, this pattern would result if the adults venturing out from one patch deplete the resource in every other patch more than in their home patch; to this end, they must be able to reach every other patch (not only neighboring patches) and  $p$  must exceed  $1 - \frac{1}{n}$ . Patterns with several occupied patches form much more readily in large metapopulations (Fig. 2). This would, in turn, correspond to multiple-cohort cycles; we are not aware of a detailed analysis of such cycles, but they may require unlikely changes of impact and sensitivity with age.

We find cycles in isolated patches also with iteroparous adults ( $\theta > 0$ ), i.e., when reproduction necessarily occurs every year and there are no isolated cohorts. These cycles are qualitatively similar to the biennial case ( $\theta = 0$ ), with the only difference that neither juveniles nor adults are fully absent in any year, only their abundances oscillate. The analysis of cycles in metapopulations where local populations are coupled by quasi-local competition (and/or dispersal) is an exciting task but beyond the scope of this paper.

## Appendix

In order to facilitate the comparison between our models and diffusive instability, here we briefly describe a model closely related to the one in Sections 2–4 but set in continuous time. Accordingly, we do not assume seasonality and a fixed-length juvenile period. Juveniles mature into adults at a constant rate  $m$ , and adults die at a constant rate  $\mu$ . For simplicity, we omit the inert egg stage, i.e. adults produce

juveniles. The population dynamics in a single patch is given by

$$\frac{dR(t)}{dt} = \alpha [R(t) f(R(t)) - \beta x R(t) - \delta y(t) R(t)]$$

$$\frac{dx(t)}{dt} = my(t) - \mu x(t)$$

$$\frac{dy(t)}{dt} = \gamma \beta R(t) x(t) - my(t) - \eta(R(t)) y(t),$$

where the notation is as in Eqs. (1)–(4). As in the main text, we assume that  $\alpha$  is large and therefore the resource is always in quasi-equilibrium. The two-patch version of this model with quasi-local competition modeled as in Eqs. (1)–(4) can exhibit pattern formation such that perturbations of the homogeneous equilibrium converge to one of the boundary equilibria.

When the resource is in quasi-equilibrium, the equations mentioned earlier reduce to a two-dimensional ODE system for  $x$  and  $y$ . For diffusive instability, the Jacobian of the ODE system should have positive and negative elements either like  $\begin{bmatrix} - & + \\ + & + \end{bmatrix}$  or like  $\begin{bmatrix} - & + \\ - & + \end{bmatrix}$ . Substituting the resource quasi-equilibrium and differentiating the equations mentioned earlier, it is easy to see that the Jacobian of our model has the signs  $\begin{bmatrix} - & + \\ ? & - \end{bmatrix}$ , where “?” can be either positive or negative. In either case, this sign structure does not conform with diffusive instability.

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