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Ideal free distributions when resources undergo population dynamics

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Abstract

This study examines the influence of optimal patch choice by consumers on resource population dynamics and on consumer distribution in a two patch environment. The evolutionarily stable strategy which describes animal distributions across habitat patches is called the ideal free distribution (IFD) strategy. Two mechanisms that lead to the IFD are: (1) direct consumer competition such as interference, and (2) exploitative competition for resources. This article focuses on the second mechanism by assuming that resources undergo population dynamics while consumer abundance is fixed. Two models of resource growth are considered in detail: the exponential and the logistic. The corresponding consumer IFD is derived for each of these two models, assuming that consumers behave adaptively by moving to the patch which provides them with the highest fitness. This derivation does not require that resources are at an equilibrium, and it provides, for each resource density, the corresponding distribution of consumers. The article suggests that adaptive patch choice by consumers decreases between patch heterogeneity in resource levels and weakens the apparent competition between resources. The results for a single consumer population are extended for two competing consumer populations. The corresponding IFD is computed as a function of the two consumer densities. This allows for the analytical description of isolegs which are the boundary lines, in the two consumer density phase space, separating regions where qualitatively different habitat preferences are predicted.

Keywords: Predator–prey dynamics; Ideal free distribution; Optimal foraging; Isoleg; Interspecific competition; Habitat selection; Resource matching

1. Introduction

The evolutionarily stable strategy (ESS; Maynard Smith, 1982) for animal distribution across habitat patches has been termed the ideal free distribution strategy (IFD, Fretwell and Lucas, 1970). It assumes that animals move freely and instantaneously between patches, they have a perfect knowledge of the qualities of all patches, and they settle in the patch which provides them with the highest resource intake rate. This results in a spatial animal distribution under which no individual can unilaterally increase its fitness by changing its strategy, and which is stable with respect to small spatial fluctuations. There are two main mechanisms that lead to the IFD. The first mechanism is direct competition among consumers (also called interference). A typical example is territorial defense. This approach does not require the inclusion of resource dynamics to derive a corresponding IFD because patch suitability is directly related to the number of consumers in that patch (Sutherland, 1983; Parker and Sutherland, 1986; Sutherland, 1996). The second mechanism is exploitative competition under which the suitability of occupied patches decreases due to the exploitation of resources. Thus, the effect of consumers on their own spatial distribution is mediated through the effect of consumers on resource densities. To model this mechanism, the resource standing crop has to be considered.

Because under the IFD, the resource intake rate is the same across all occupied patches this allows derivation of the "input matching rule" (Parker, 1978; Sutherland, 1996) which states that the ratio of resource input rates "matches" the consumer distribution across occupied patches. This rule was derived for "continuous systems" in which resources are immediately consumed upon their arrival in the system and there is a zero standing crop in either patch (Parker and Stuart, 1976; Parker,

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1978; Milinski and Parker, 1991). Lessells (1995) extended Parker's rule to situations in which resources exist at positive levels. She assumed that resources are input to patches at a fixed rate and that demographic forces together with resource consumption drive resources to an equilibrium. Then she showed that the Parker's matching rule also holds at this equilibrium. Recently, Adler et al. (2001) studied the IFD for size structured populations under various additional constraints such as the presence of predators, competition, and two limiting food resources.

Contrary to these matching rules, I derive in this article a matching rule which does not assume that the population numbers are at an equilibrium. I focus on the case in which a fixed number of consumers compete for two resources located in spatially separated patches. The case in which both resources and consumers are dynamic variables was considered by Křivan (1997). The assumption of fixed consumer numbers is realistic provided resource generation times are much shorter than is the generation time of consumers which is the case of many natural systems including that of herbivores. Assuming that consumers are omniscient and they move to the patch which provides them with the highest resource input rate I study resource dynamics and consumer distributions without assuming a resource equilibrium. I will derive a matching rule for non-equilibrium population dynamics and I will study the effect of consumer adaptive behavior on apparent competition between the two resource types (Holt, 1977). Moreover, I will also study effects of the adaptive consumer patch choice on the resource heterogeneity across patches.

The IFD for a single species can be extended for two or more competing species (Lawlor and Maynard Smith, 1976; Possingham, 1992; Grand and Dill, 1999, Grand, 2002; Guthrie and Moorhead, 2002; Křivan and Sirot, 2002). For two competing species it can be graphically analysed by using isolegs, which are the lines separating regions of the two consumer phase space where qualitatively different habitat preferences are observed (Rosenzweig, 1979,1981,1991). In general, for each of the two consumer species many isolegs can be defined. Following Křivan and Sirot (2002) I use two prominent ones. Consider one of the two consumer species. The first isoleg, which delimitates the part of the consumer phase space in which the species specializes in patch 1, is called the 0% isoleg. The second isoleg, which delimitates specialization in patch 2, is called the 100% isoleg. Křivan and Sirot (2002) derived the IFD for two species assuming that the individual fitness is derived from the classic Lotka–Volterra competition model which considers consumer dynamics but does not consider resource dynamics. They showed that isolegs are piece-wise linear and that for high levels of interspecific competition the IFD cannot be uniquely predicted in some regions of the population density space because two possible distributions exist. This is not surprising because the Lotka–Volterra competition model predicts multiple population equilibria for high levels of interspecific competition. In this article I derive the IFD for the resource exploitation model (Tilman, 1982) which considers resource dynamics instead of consumer dynamics.

2. The IFD for a single population

In this section I consider two simple models of reproducing resources. The first model assumes that resource growth is unlimited and that it is described by the exponential function while the second model assumes logistic resource growth. For simplicity assume that handling times are zero and functional responses are linear. These assumptions allow for a great deal of insight, but along the same lines more complicated systems can be analyzed too (non-zero handling times, more patches, other types of resource growth rates, etc.). The choice of the two simple examples presented here is mainly to illustrate the methodological approach which is applicable to more complex situations as well.

2.1. *Exponential resource growth*

Consider two patches with resource densities R_1 and R_2, respectively. Assume that these resources grow exponentially with intrinsic per capita growth rates r_1 and r_2. The overall consumer density is C and assume that consumers can freely and instantaneously move between the two patches. The corresponding Lotka–Volterra system is described by the following model:

$$\begin{aligned}\frac{dR_1}{dt} &= R_1(r_1 - \lambda_1 u_1 C),\\ \frac{dR_2}{dt} &= R_2(r_2 - \lambda_2 u_2 C),\end{aligned} \qquad (1)$$

where u_i is the proportion of the consumer population currently in patch i and λ_i is the cropping rate. Thus $C_i = u_i C$ denotes the consumer abundance in patch i $(i = 1, 2)$. At the individual level, u_i describes the preference of a consumer for patch i measured by the time an average consumer would spend in this patch in its lifetime. For adaptive consumers u_i is not fixed but it changes as the resource levels change. As the travel time between patches is zero, I have $u_1 + u_2 = 1$. In what follows the patch suitability is measured by the food intake rate in that patch. Assuming a linear functional response, the quality of patch i is described by $\lambda_i R_i$. Provided that consumers are equal competitors and there are no other constraints (such as those discussed by Adler et al., 2001) this leads to the following animal strategy: If patch 1 is more profitable than patch 2 $(\lambda_1 R_1 > \lambda_2 R_2)$ then consumers should spend all their time in patch 1 $(u_1 = 1)$, and, conversely. If the two patches are of the same suitability ($\lambda_1 R_1 = \lambda_2 R_2$) then the consumer strategy is not uniquely given. Note that this is exactly the case for which I will derive below a corresponding input matching rule, because only under this condition are both patches inhabited. However, the assumption of omniscient consumers alone does not readily provide us with any matching rule. In order to derive a matching rule, I need to consider resource dynamics described by Eq. (1). In this section assume, without any loss of generality, that the intrinsic per capita resource growth rate in patch 1 is higher than in patch 2, i.e.,

$$r_1 > r_2.$$

If consumer density is low

$$C < \frac{r_1 - r_2}{\lambda_1} \tag{2}$$

then predation pressure is not strong enough to drive resources to the level at which patch suitabilities equalize (Appendix A) and all consumers eventually occupy the patch with the higher intrinsic resource growth rate which is patch 1 in our case (Fig. 1). Corresponding resource population dynamics are shown in Fig. 2A. Depending on the initial resource population densities, consumers upon introduction distribute either to patch 1 (if the initial resource densities are below the dashed line in Fig. 2) or to patch 2 (if the initial resource densities are above the dashed line). I remark that the dashed line describes the resource levels which make both patches equally profitable for consumers. In the first case consumers stay in patch 1 forever, because their density is not high enough to decrease the resource level in patch 2 so that both patches are equally profitable. In the case where, initially, the resource density in patch 2 is high, consumers move to this patch which, in turn, decreases the standing crop there to the level which makes both patches equally profitable for consumers. At this moment, all consumers move to patch 1 where they stay forever (Fig. 2A). Because the consumer density is low, consumers cannot control resource growth and resources in both patches increase exponentially. I conclude that when at low numbers, consumers prefer, in the long run, the patch with the higher intrinsic resource growth rate.

Next consider the situation in which the consumer density is so high that inequality (2) is reversed. Depending on the initial resource densities, consumers after introduction move to the more profitable patch. If the initial resource densities are above the dashed line (see Fig. 2B) consumers move to patch 2, if they are below the dashed line then consumers move to patch 1. The presence of consumers in either patch decreases resource growth in that patch so that, after some time, resources reach levels at which both patches are equally profitable for consumers. Contrary to the case of low

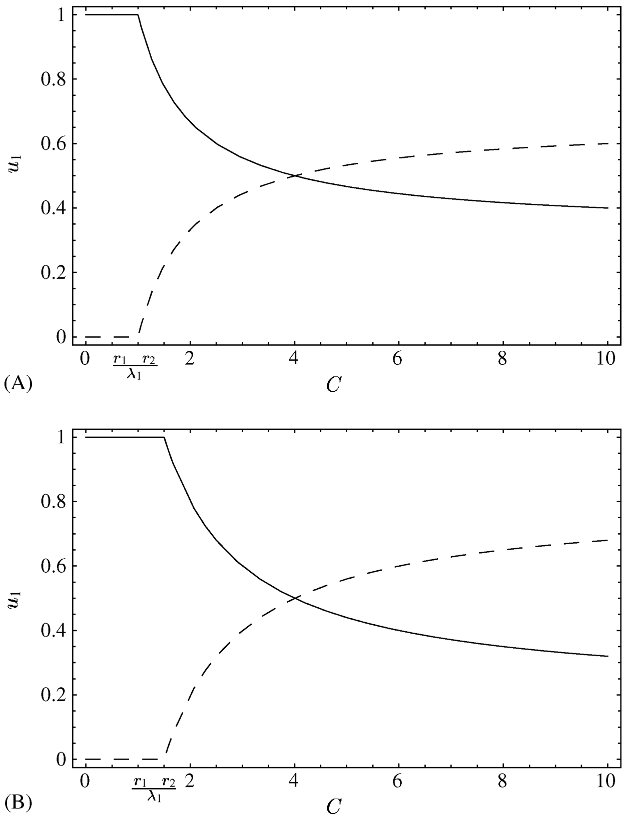

Fig. 1. Consumers patch preferences as a function of the total consumer density. For low consumer densities all consumers are in the more suitable patch 1. For higher consumer densities consumers spread over the two patches. (A) is for exponentially growing resources ($r_1 = 2$, $r_2 = 1$, $\lambda_1 = 1$, $\lambda_2 = 0.5$) while (B) is for logistically growing resources ($r_1 = 2$, $r_2 = 1$, $\lambda_1 = 1$, $\lambda_2 = 0.5$, $K_1 = 20$, $K_2 = 10$). Solid and dashed lines show preferences for patch 1 and patch 2, respectively.

consumer densities, the consumer density is now high enough to keep resources in both patches at the levels that neither of them becomes more profitable. Technically speaking, in the resource density phase space, the trajectories of model (1) are pushed from both sides to the equal profitability line (the dashed line in Fig. 2; Appendix A). Thus, any spatial perturbation in the consumer distribution is swept away and the resource densities return to the dashed line. This is the consequence of the fact, that the consumer density is high enough to keep resource densities in both patches at such levels to make both patches equally profitable for consumers. The fact that resource dynamics are such that both patches are equally profitable ($\lambda_1 R_1 = \lambda_2 R_2$) allows derivation of the proportion of consumers in patch 1:

$$u_1 = \frac{r_1 - r_2 + \lambda_2 C}{(\lambda_1 + \lambda_2)C} \tag{3}$$

and in patch 2

$$u_2 = \frac{r_2 - r_1 + \lambda_1 C}{(\lambda_1 + \lambda_2)C}, \tag{4}$$

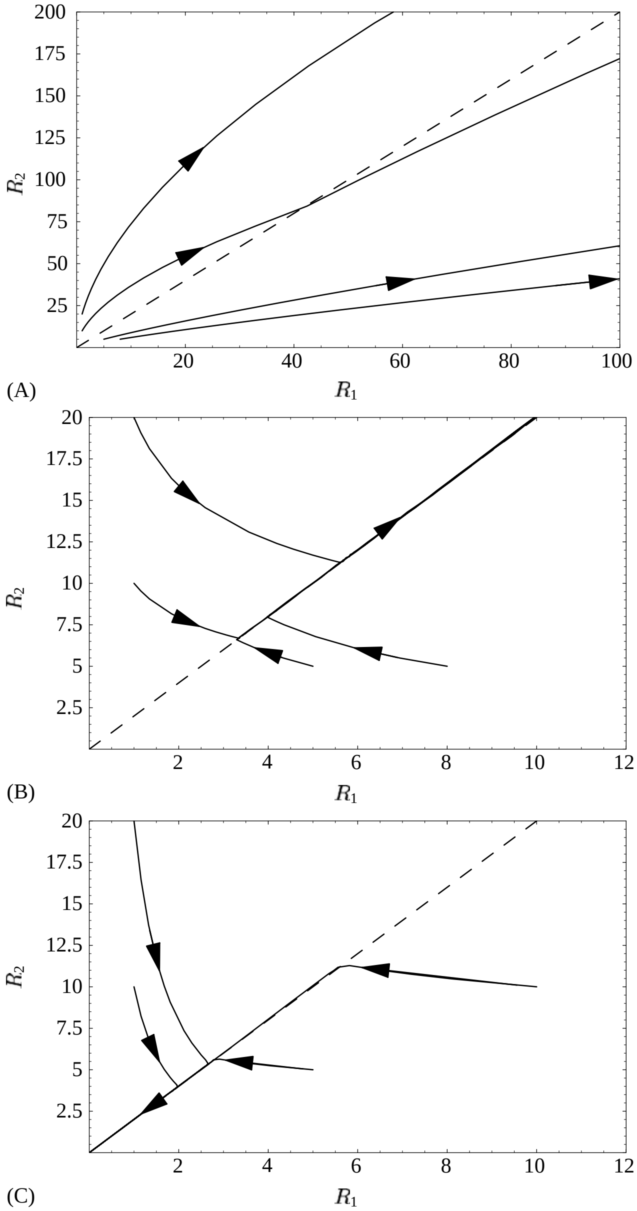

Fig. 2. Resource dynamics (R_1 = resource in patch 1, R_2 = resource in patch 2) when resources grow exponentially. In (A) the consumer population is low ($C = 0.3$) and all consumers move eventually to the patch with a higher intrinsic growth rate. In (B) the consumer population is intermediate ($C = 3$) and it splits over the two patches while resources are growing. In (C) the consumer population is large ($C = 6$) and it drives resources in both patches to extinction. The dashed line (the IFD line) denotes the resource densities for which the two patches are equally profitable for consumers. Parameters: $r_1 = 1.5, r_2 = 1, \lambda_1 = 1, \lambda_2 = 0.5$.

see Appendix A and Fig. 1. I get the following "matching rule"

$$\frac{C_1}{C_2} = \frac{u_1}{u_2} = \frac{r_1 - r_2 + \lambda_2 C}{r_2 - r_1 + \lambda_1 C}.$$

This matching rule depends on the intrinsic resource growth rates, consumers cropping rates and on the overall consumer density. Note that if the two resources were exactly the same ($r_1 = r_2, \lambda_1 = \lambda_2$) then $C_1/C_2 = 1$, i.e., consumers distribute equally over the two patches. Unequal distributions of consumers are due to differences in the two resources.

Substituting the consumer IFD described by (3) and (4) in model (1) gives resource population dynamics at the consumers IFD:

$$\begin{aligned} \frac{dR_1}{dt} &= R_1 \frac{\lambda_1 \lambda_2}{\lambda_1 + \lambda_2}\left(\frac{r_1 \lambda_2 + r_2 \lambda_1}{\lambda_1 \lambda_2} - C\right), \\ \frac{dR_2}{dt} &= R_2 \frac{\lambda_1 \lambda_2}{\lambda_1 + \lambda_2}\left(\frac{r_1 \lambda_2 + r_2 \lambda_1}{\lambda_1 \lambda_2} - C\right). \end{aligned} \tag{5}$$

This implies that for

$$\frac{r_1 - r_2}{\lambda_1} < C < \frac{r_1 \lambda_2 + r_2 \lambda_1}{\lambda_1 \lambda_2}$$

resources are exponentially increasing in both patches despite their consumption by consumers (Fig. 2B). For high consumer densities satisfying

$$\frac{r_1 \lambda_2 + r_2 \lambda_1}{\lambda_1 \lambda_2} < C$$

consumers drive resource levels in both patches to zero (Fig. 2C). When

$$C = \frac{r_1 \lambda_2 + r_2 \lambda_1}{\lambda_1 \lambda_2} \tag{6}$$

every point on the IFD line (the dashed line in Fig. 2) is an equilibrium point. This means that once resource densities reach the level under which both patches are equally profitable (i.e., the dashed line in Fig. 2) then they do not change anymore. Of course, equality (6) is unrealistic but for consumer densities which are close to this critical value changes in resource abundances will be very slow.

The model with exponential resource growth and adaptive consumers predicts that for all consumer densities and all combination of parameters there are only two possibilities with respect to resource population dynamics: either resources in both patches grow exponentially, or they are depleted. Now I compare this result with a system in which consumers do not behave adaptively, i.e., their preferences for either patch are fixed and independent of the resource standing crop. For the latter case there are the following qualitative possibilities: for low consumer densities both resources grow exponentially, for intermediate consumer densities the resource with lower ratio r_i/λ_i is depleted due to apparent competition via shared consumers (Holt, 1977) and the other resource grows exponentially, and for high consumer densities both resources are depleted. This suggests that adaptive consumer behavior tends to decrease resource heterogeneity measured by the ratio R_1/R_2 of resource levels in the two patches. Indeed, this ratio is given for non-adaptive consumers (with fixed patch preferences u_i) by

$$\frac{R_1(t)}{R_2(t)} = e^{(r_1 - \lambda_1 u_1 C - (r_2 - \lambda_2 u_2 C))t}.$$

If $r_1 - \lambda_1 u_1 C > r_2 - \lambda_2 u_2 C$ then this ratio tends to infinity, while the same ratio for adaptive consumers is constant and given by λ_2/λ_1 (because when the resources are suppressed to the level where both patches are equally profitable for consumers, $R_1/R_2 = \frac{\lambda_2}{\lambda_1}$). Similarly, if $r_1 - \lambda_1 u_1 C < r_2 - \lambda_2 u_2 C$ then the above ratio tends to zero, while the same ratio for adaptive consumers is again constant. This implies that adaptive consumer behavior decreases resource heterogeneity among patches.

2.2. Logistic resource growth

The assumption on exponential resource growth is not realistic if resources are limited also by bottom up forces. For this reason I compute the IFD for the case in which resources grow logistically. Model (1) becomes

$$\begin{aligned} \frac{dR_1}{dt} &= r_1 R_1 \left(1 - \frac{R_1}{K_1}\right) - \lambda_1 u_1 C R_1, \\ \frac{dR_2}{dt} &= r_2 R_2 \left(1 - \frac{R_2}{K_2}\right) - \lambda_2 u_2 C R_2 \end{aligned} \qquad (7)$$

and the consumer strategy is the same as in the previous section. If there are no consumers ($C = 0$) then the resource level in either patch reaches its environmental carrying capacity K_i ($i = 1, 2$). Without loss of generality assume that $K_1\lambda_1 > K_2\lambda_2$ which implies that for low consumer densities patch 1 is more profitable than patch 2 and the interior resource equilibrium of system (7) without any consumers is below the dashed line (Fig. 3A). When consumers are introduced, the resource equilibrium shifts to the left (Fig. 3B) because the resource 1 equilibrium density decreases as consumers prefer to stay in patch 1. Moreover, isoclines (dotted lines in Fig. 3) become discontinuous (cf. Fig. 3A vs. Fig. 3B, and C). The corresponding resource equilibrium with consumers present is

$$R_1^\star = K_1 \left(1 - \frac{\lambda_1}{r_1} C\right),$$

and

$$R_2^\star = K_2,$$

(Fig. 3B). This is so until the consumer density reaches the critical density

$$C^\star = \frac{r_1(K_1\lambda_1 - K_2\lambda_2)}{K_1\lambda_1^2}. \qquad (8)$$

At this critical consumer density, the resource equilibrium is exactly on the IFD line and both patches are equally suitable for consumers. It can be proved that for consumer densities higher than the critical density $C^\star$ the corresponding resource equilibrium cannot leave the IFD line, because consumer densities are high enough to equilibrate suitability of both patches. The consumer population splits across the two patches in such a way that the fitness of individuals in either patch is the same

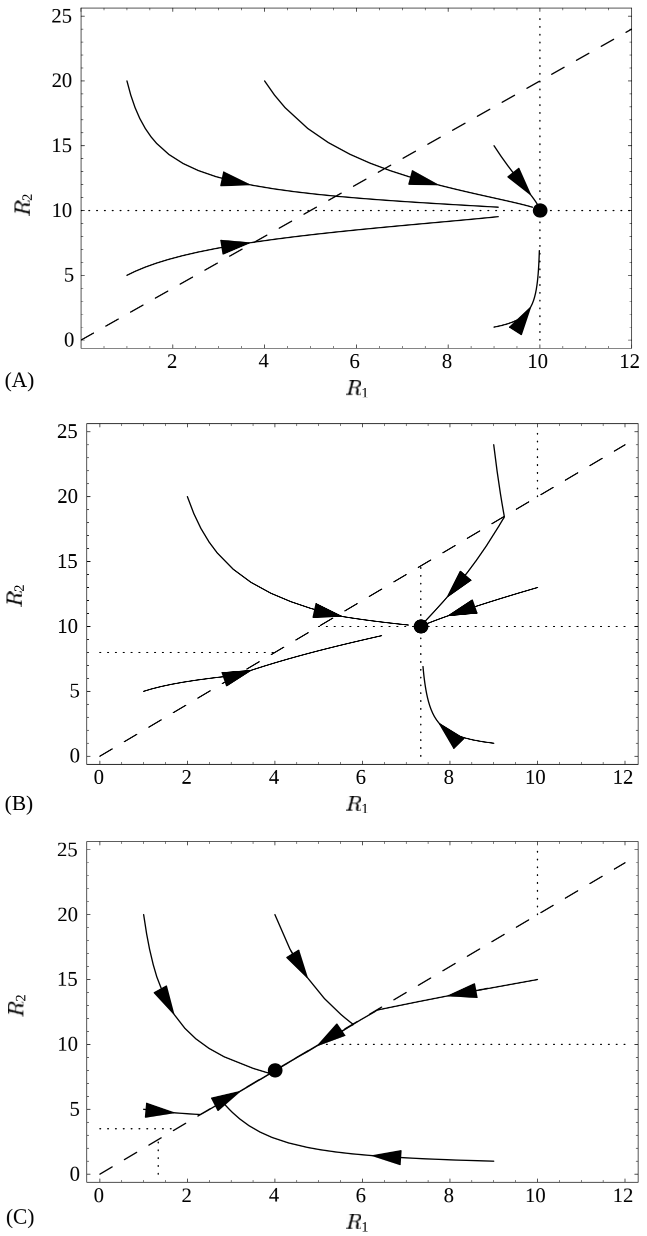

Fig. 3. Resource dynamics when resources grow logistically. In (A) no consumers are present ($C = 0$) and resources reach environmental carrying capacities K_1 and K_2. The dashed line denotes the resource densities for which the two patches are equally profitable for consumers. In (B) the consumer population is low ($C = 0.4$) and all consumers move eventually to the more suitable patch 1 (the patch with higher value $\lambda_i K_i$). This leads to a decreased equilibrium resource density in this patch and the resource equilibrium moves toward the dashed line. In (C) the consumer population is large enough ($C = 1.3$) and it splits over the two patches. The adaptive behavior of consumers keeps the resource equilibrial densities at the dashed line. Parameters: $r_1 = 1.5, r_2 = 1, K_1 = 10, K_2 = 10, \lambda_1 = 1, \lambda_2 = 0.5$.

(Appendix B, Fig. 3C). This is so for all consumer densities which are higher than the critical value given by $C^{\star}$. The corresponding resource equilibrium densities are given by

$$R_1^{\star} = \frac{K_1K_2\lambda_2(r_2\lambda_1 + r_1\lambda_2 - C\lambda_1\lambda_2)}{K_1r_2\lambda_1^2 + K_2r_1\lambda_2^2}$$

and

$$R_2^{\star} = \frac{\lambda_1}{\lambda_2}R_1^{\star},$$

(Appendix B). These resource equilibrial densities are positive if

$$C < \frac{r_2\lambda_1 + r_1\lambda_2}{\lambda_1\lambda_2}. \tag{9}$$

If the opposite inequality holds, resources in both patches are depleted because of heavy consumption. Fig. 3C shows that resource densities are driven to the IFD line and when they reach it they move along it towards the equilibrium. The corresponding "matching principle" which relates the proportion of consumers in the two patches at the resource equilibrium is given by (Appendix B)

$$\frac{u_1}{u_2} = \frac{r_1r_2(\lambda_2K_2 - \lambda_1K_1) - C\lambda_2^2r_1K_2}{r_1r_2(\lambda_1K_1 - \lambda_2K_2) - C\lambda_1^2r_2K_1}.$$

If $K_1\lambda_1$ is not very different from $K_2\lambda_2$, or C is not too low, the above matching principle can be approximated by

$$\frac{u_1}{u_2} \sim \frac{r_1K_2\lambda_2^2}{r_2K_1\lambda_1^2}.$$

Once again, the above results suggest that there are only two possibilities with respect to the long-term resource population dynamics. Either the consumer density is such that it allows positive equilibrial resource densities in both patches, or, for high consumer densities resources in both patches are depleted. This is a similar result as in the case for exponentially growing resources. The consumer IFD is reached at the population equilibrium provided the consumer density is above the critical threshold given by formula (8).

Now I compare these results with resource dynamics when consumers are non-adaptive. For non-adaptive consumers with fixed preferences for either patch the corresponding equilibrial resource densities are given by

$$\frac{K_i(r_i - \lambda_iu_iC)}{r_i}, \quad i = 1,2.$$

This implies that for low consumer densities equilibrial resource levels in both patches are positive, for intermediate consumer densities resources in one patch are depleted while they are kept at a positive equilibrium in the other patch, and for high consumer densities resources in both patches are depleted. For adaptive consumers the case in which only one patch is depleted cannot happen. This implies that adaptive consumer behavior weakens the apparent competition between resources and that adaptive consumer behavior tends to decrease spatial heterogeneity between resources.

Another observation is that resource densities are positive in systems with adaptive consumers for consumer densities for which non-adaptive behavior implies resource extinction at least in one patch. Indeed, resource equilibrial densities in systems with non-optimal consumers are positive if

$$C < \min\left\{\frac{r_1}{u_1\lambda_1}, \frac{r_2}{u_2\lambda_2}\right\}.$$

When consumers are adaptive, equilibrial resource densities are positive if inequality (9) holds. Because for all u_i between zero and one

$$\min\left\{\frac{r_1}{u_1\lambda_1}, \frac{r_2}{u_2\lambda_2}\right\} \leqslant \frac{r_2\lambda_1 + r_1\lambda_2}{\lambda_1\lambda_2}$$

this implies that when consumer behavior is adaptive, resources coexist at a positive equilibrium density for such consumer densities for which they could not coexist if consumers were non-adaptive because of apparent competitive exclusion (Holt, 1977).

2.3. Comparison with Parker's matching rule

Parker (1978) derived an input matching rule which relates the consumer distribution to patch resource input rates for continuous input systems. For the case in which resources are not consumed immediately, i.e., when there is a standing resource crop, Parker's rule was extended by Lessells (1995). Now I will compare matching rules predicted by my models with those of Parker and Lessells. First, consider a continuous input system with no standing resource crop, which is the condition under which Parker matching rule applies. His rule assumes that the resource input rate to patch i is given by S_i and that consumers are at the IFD. As the per capita consumer intake rate $S_i/(u_iC)$ $(i = 1,2)$ should be the same in both patches I get Parker's matching rule:

$$\frac{u_1}{u_2} = \frac{C_1}{C_2} = \frac{S_1}{S_2}.$$

When there is a positive standing resource crop, Lessells (1995) extended the above matching rule by assuming that resources are input to a patch at a constant rate and that the standing resource crop settles at an equilibrium. In fact, her argument can be also extended to my systems which do not assume a constant resource input. Let $r_i(R_i)$ denote the growth of resources and f_i the functional response in patch i, i.e., the resource dynamics in patch i are described by

$$\frac{dR_i}{dt} = r_i(R_i) - f_i(R_i)u_iC.$$

Assuming that population dynamics are such that resources converge to an equilibrium $R_i^{\star}$, I obtain at the equilibrium

$$r_i(R_i^{\star}) = f_i(R_i^{\star})u_iC, \quad i = 1,2.$$

If I assume that consumers are distributed across both patches then, according to the IFD, per capita consumer intake rate of resources must be the same in both patches, i.e.,

$$f_1(R_1^{\star}) = f_2(R_2^{\star}).$$

This implies the following input matching rule:

$$\frac{u_1}{u_2} = \frac{r_1(R_1^{\star})}{r_2(R_2^{\star})}.$$

Thus, this rule provides the same input matching rule as I obtained for the logistically growing resources, because in this case resource dynamics settle at an equilibrium. However, the above matching rule does not predict the IFD for exponentially growing resources, because resources do not settle at an equilibrium in this case. My approach presented in this article, when compared with the Parker's matching principle is more general, because it is not limited to the case in which resources settle at an equilibrium and it allows us to compute patch preferences for non-equilibrium resource densities. Thus, it can be used to study population dynamics even if they do not converge to equilibrial densities (Křivan, 1997; Boukal and Křivan, 1999; van Baalen et al., 2001).

3. IFD for two competing species

Now I will extend the previous analysis to the case of two competing consumer species. Thus, instead of a single consumer with density C, I consider two competing species whose overall densities are denoted by N and P. Again I assume that the densities of these two species are constant in time and the resource level in patch 1 is R_1 and in patch 2 is R_2. The extension of model (1) in a two consumer environment is described by the following population dynamics:

$$\begin{aligned}\frac{dR_1}{dt} &= r_1R_1\left(1 - \frac{R_1}{K_1}\right) - \lambda_{N_1}u_1NR_1 - \lambda_{P_1}v_1PR_1,\\ \frac{dR_2}{dt} &= r_2R_2\left(1 - \frac{R_2}{K_2}\right) - \lambda_{N_2}u_2NR_2 - \lambda_{P_2}v_2PR_2.\end{aligned} \tag{10}$$

In this model resources in both patches without consumers grow logistically with intrinsic per capita growth rates r_i and carrying capacities K_i $(i = 1,2)$. Parameters $\lambda_{N_1}, \lambda_{N_2}, \lambda_{P_1}, \lambda_{P_2}$ are resource cropping rates where the first subindex refers to a species and the second to a patch. Controls u_1 (v_1) and u_2 (v_2) describe the average proportion of a lifetime that an individual of the first (second) consumer species spends in patch 1 and in patch 2, respectively. Thus, $u_1 + u_2 = v_1 + v_2 = 1$. My aim is to derive these controls for each population density of species N and P. To approach this problem, I need to define a fitness measure for these two species. Following the case of a single consumer population I assume that individual fitness is directly proportional to the food intake rate which gives

$$W_N = \lambda_{N_1}u_1R_1 + \lambda_{N_2}u_2R_2$$

for species N and

$$W_P = \lambda_{P_1}v_1R_1 + \lambda_{P_2}v_2R_2$$

for species P. Maximization of these fitness functions gives the optimal strategy for the two species. If $\lambda_{N_1}R_1 > \lambda_{N_2}R_2$ then individuals of species N should stay in patch 1, while if the opposite inequality holds they should stay in patch 2 and similarly for species P. By patch switching consumers can, if their density is high enough, suppress resource levels in the two patches so that both patches give the same fitness. On the contrary to the case of a single consumer population there are now two switching lines; one for species N (the dotted line in Fig. 6A) and one for species P (the dashed line in Fig. 6A). The qualitative analysis depends on the position of these two switching lines. Without loss of generality I will assume that

$$\frac{\lambda_{N_1}}{\lambda_{N_2}} < \frac{\lambda_{P_1}}{\lambda_{P_2}} \tag{11}$$

which means that the switching line for species N is (in the resource (R_1, R_2) phase space) below the switching line for species P (which is the case shown in Fig. 4). Thus, consumers N switch from patch 1 to patch 2 at lower densities of resource 2 than consumers P if the density of resource 1 is the same. Analysis of Appendix C shows that provided densities of species N and P are not too high, one positive resource equilibrium of model (10) exists. This equilibrium corresponds either to one of three “pure” consumer species distributions (all individuals of both species are in patch 1, and all individuals of species N are in patch 2 and all individuals of species P are in patch 1, and all individuals of both species are in patch 2) or to one of the two “mixed” distributions under which one species occupies both patches. Note that because of assumption (11) the case in which all individuals of species N occupy patch 1 and all individuals of species P occupy patch 2 is impossible (because in this case the inequalities $\lambda_{N_1}R_1 > \lambda_{N_2}R_2$ and $\lambda_{P_1}R_1 < \lambda_{P_2}R_2$ cannot hold simultaneously).

Now I will study isolegs, which are the lines separating regions in the consumer phase space where qualitatively different habitat preferences are observed (Rosenzweig, 1979,1981,1991). Křivan and Sirot (2002) analyzed the 0% isoleg (the curve which delimitates in the consumer phase space specialization in habitat 1) and the 100% isoleg (the curve which delimitates specialization in habitat 2) for the Lotka–Volterra

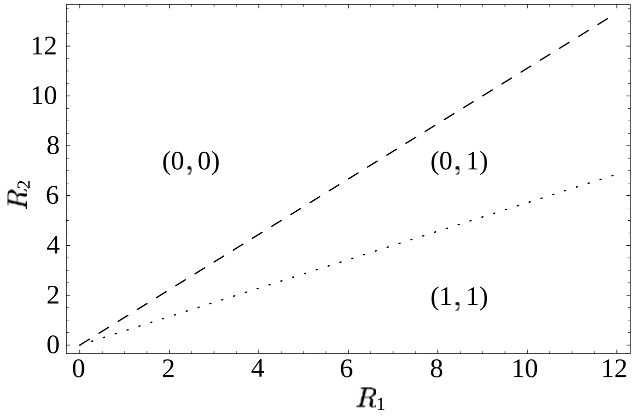

Fig. 4. This figure shows the possible consumer preferences for habitats (the first number shows preference of species N for patch 1 and the second number shows the preference of species P for patch 1) in the resource density phase space provided inequality (11) holds. The dashed line denotes the resource densities for which the fitness of consumer P is the same in both patches and the dotted line denotes the resource densities for which the fitness of consumer N is the same in both patches.

model of two competing species. Their model assumed that consumer populations undergo population dynamics but the resources are constant. In this article I consider the opposite case: resources undergo population dynamics but consumers do not. I will study two cases: one patch is more profitable for both consumer species (shared preferences), and each consumer species prefers different patch (distinct preferences).

3.1. *The shared-preference case*

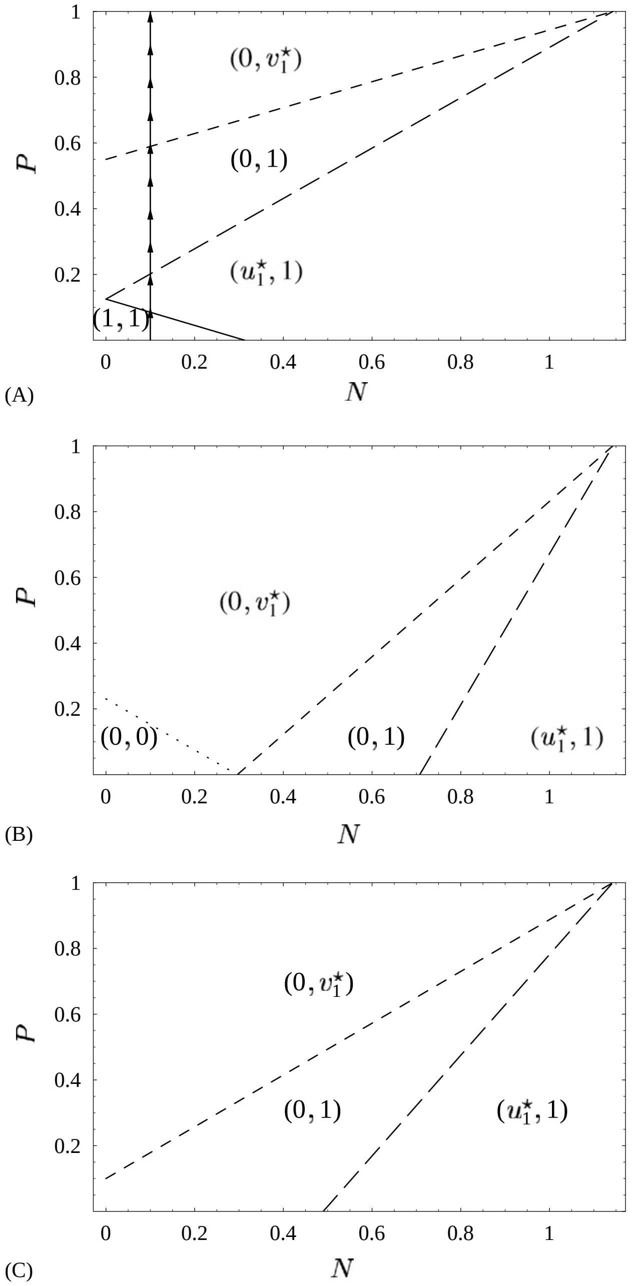

Fig. 5. Patch selection maps for two competing species in a two patch environment. The 0% (solid line) and the 100% (long-dashed line) isolegs for species N and the 0% (dashed line) and the 100% (dotted line) isolegs for species P separate regions with qualitatively different species distributions. Proportions of species N (u_1) and P (v_1) in the first patch are given in parentheses. In (A) the first patch is better for both species at low densities ($\lambda_{P_1}/\lambda_{P_2} > \lambda_{N_1}/\lambda_{N_2} > K_2/K_1,\ K_2 = 5$), in (B) the second patch is better for both species at low densities ($K_2/K_1 > \lambda_{P_1}/\lambda_{P_2} > \lambda_{N_1}/\lambda_{N_2},\ K_2 = 15$), and in figure (C) the first patch is better for species P and the second patch is better for species N when at low densities ($\lambda_{P_1}/\lambda_{P_2} > K_2/K_1 > \lambda_{N_1}/\lambda_{N_2},\ K_2 = 10$). Other parameters: $\lambda_{N_1} = 0.4,\ \lambda_{N_2} = 0.7,\ \lambda_{P_1} = 1,\ \lambda_{P_2} = 0.9,\ r_1 = 1,\ r_2 = 0.8,\ K_1 = 10$.

Here I consider the case in which both consumer species prefer the same patch at low densities. At very low consumer densities resources almost reach their carrying capacities and the fitness of species N is given approximately by

$$W_N = \lambda_{N_1} u_1 K_1 + \lambda_{N_2} u_2 K_2$$

and the fitness of species P by

$$W_P = \lambda_{P_1} v_1 K_1 + \lambda_{P_2} v_2 K_2.$$

Firstly I assume that patch 1 is more profitable than patch 2 for both species. This means that at low consumer densities the fitness of both species is higher in patch 1 than in patch 2 (i.e., $\lambda_{N_1} K_1 > \lambda_{N_2} K_2$ and $\lambda_{P_1} K_1 > \lambda_{P_2} K_2$) so that all individuals prefer this patch. Due to inequality (11) this happens provided

$$\frac{\lambda_{N_1}}{\lambda_{N_2}} > \frac{K_2}{K_1}.$$

Under this assumption there are three isolegs whose position is qualitatively the same as shown in Fig. 5A. There is the 0% isoleg for species N (solid line), the 100% isoleg for species N (long-dashed line) and the 0% isoleg for species P (short-dashed line). For low consumer densities (lower left corner) individuals of both species occupy the more profitable patch 1. Let us consider IFD along a gradient in species P density (see the transect line in Fig. 5A). As density of species P increases the resource level in patch 1 decreases while it stays constant in patch 2 (because all consumers are in patch 1; Fig. 6, segment of the solid line I). For some density of species P the resource equilibrium reaches the switching line $\lambda_{N_1}R_1 = \lambda_{N_2}R_2$ (the dotted line in Fig. 6A). At this moment both patches become equally profitable for species N and this population splits across them in the ratio

$$\frac{u_1}{u_2} = \frac{K_2 r_1 \lambda_{N_2}(N\lambda_{N_2} - r_2) + K_1 r_2 \lambda_{N_1}(r_1 - P\lambda_{P_1})}{r_2(K_2 r_1 \lambda_{N_2} + K_1 \lambda_{N_1}(N\lambda_{N_1} + P\lambda_{P_1} - r_1))},$$

see Appendix C. As density of species P increases further, the resource levels decrease in both patches because more individuals of species N move to patch 2 due to strong competition in patch 1 (Fig. 6, segment II). The resource equilibrium “slides” downwards along the switching line $\lambda_{N_1}R_1 = \lambda_{N_2}R_2$. At some density of species P all individuals of species N are in patch 2 while all individuals of species P still occupy patch 1 only. As density of species P increases further on, the resource level in patch 1 decreases (Fig. 6A, segment III) and for a critical density of species P the fitness for individuals of this species will be the same in both patches. This corresponds to the moment where the resource equilibrium reaches the switching line $\lambda_{P_1}R_1 = \lambda_{P_2}R_2$ (dashed line in Fig. 6A). Since then on, both patches are equally profitable for species P and this species spreads over them in the ratio

$$\frac{v_1}{v_2} = \frac{r_1(K_2\lambda_{P_2}(r_2 - N\lambda_{N_2} - P\lambda_{P_2}) - K_1 r_2 \lambda_{P_1})}{K_1 r_2 \lambda_{P_1}(r_1 - P\lambda_{P_1}) + K_2 r_1(N\lambda_{N_2} - r_2)\lambda_{P_2}},$$

Appendix C. As the density of species P increases, resources in both patches will be depleted (Fig. 6A, segment IV). A similar analysis can be done for any transect.

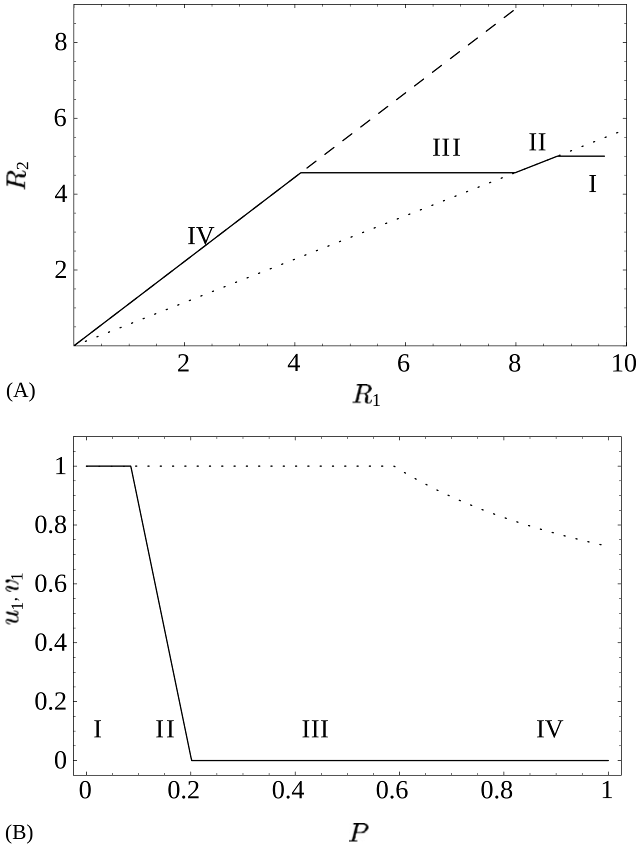

Fig. 6. (A) shows dependence of the resource interior equilibrium and (B) dependence of the consumer distribution (solid line shows the proportion of consumer N in patch 1 and the dotted line shows the proportion of consumer P in patch 1, respectively) along the transect from Fig. 5A. When consumers are at very low densities, resources reach approximately their environmental carrying capacities ($K_1 = 10, K_2 = 5$, (A, section I) and both consumer species are in the more profitable patch 1 (B, section I). As density of species P increases, resource 1 equilibrium decreases and it reaches the switching line ($\lambda_{N_1}R_1 = \lambda_{N_2}R_2$). Because both resource patches are equally profitable for consumer N, individuals of species N will inhabit also patch 2 while patch 1 is still better for species P (section II). As density of species P increases, species 1 is competed out of patch 1 and it occupies patch 2 only (section III). The resource level in patch 1 decreases and when it reaches the second switching line ($\lambda_{P_1}R_1 = \lambda_{P_2}R_2$) both patches will be equally profitable for species P which spreads over them (section IV). Parameters are the same as in Fig. 5A.

Secondly, I assume that patch 2 is more profitable for both species (i.e., $\lambda_{N_1}K_1 < \lambda_{N_2}K_2$ and $\lambda_{P_1}K_1 < \lambda_{P_2}K_2$). This is the case where

$$\frac{K_2}{K_1} > \frac{\lambda_{P_1}}{\lambda_{P_2}} > \frac{\lambda_{N_1}}{\lambda_{N_2}}.$$

In this case I observe the 100% isoleg for species N (long-dashed line in Fig. 5B) and the 0% (short-dashed line in Fig. 5B) and the 100% (dotted line in Fig. 4B) isolegs for species P. When at low densities both species occupy the more profitable patch 2.

3.2. The distinct-preference case

Here assume that at low consumer densities patch 1 is more profitable for species N (i.e., $\lambda_{N_1}K_1 > \lambda_{N_2}K_2$) while patch 2 is more profitable for species P (i.e., $\lambda_{P_1}K_1 < \lambda_{P_2}K_2$). This happens provided

$$\frac{\lambda_{P_1}}{\lambda_{P_2}} > \frac{K_2}{K_1} > \frac{\lambda_{N_1}}{\lambda_{N_2}}.$$

In this case there are only two isoclines (Appendix C): the 100% isocline for species N (long-dashed line in Fig. 5C) and the 0% isocline for species P (short-dashed line in Fig. 5C). For low species densities (lower left corner) species N occupies patch 1 and species P occupies patch 2.

4. Discussion

Assuming constant consumer numbers, I developed models of the IFD in a two patch environment where resources undergo population dynamics. On contrary to some previous studies on IFD that assumed either zero standing resource crop (Parker and Stuart, 1976; Parker, 1978; Milinski and Parker, 1991), or convergence of resources to an equilibrium (Lessells, 1995), the methodology used in this article allows derivation of the IFD for the case in which there is a standing resource crop that undergoes population dynamics. Most models assume that the IFD is reached due to a decreased resource intake rate when number of consumers increases, e.g., due to consumer interference (Fretwell and Lucas, 1970; Sutherland, 1996). In this approach the resource dynamics are not considered, because the competition among consumers is directly related to the number of consumers. On the contrary, the mechanism which drives the consumer distribution outlined in this article is based on exploitative competition. To derive the corresponding IFD is more complicated than in the case in which resources are kept at constant densities because resource dynamics must be considered. In fact, there is a feedback loop between the consumer distribution and the resource densities. The resource densities are influenced by the consumer distribution which, in turn, depends on the resource densities. In this article I have assumed a linear functional response, which allows for simple analytical treatment of the resulting models, but the same methodology can be applied to more realistic functional responses (such as Holling type II functional response). I have proved that optimal patch choice by consumers tends to decrease inter-patch heterogeneity. In particular, when consumers are adaptive then there are only two qualitatively different resource population dynamics: either resources coexist in both patches, or they are driven simultaneously to extinction. The case in which resources are driven to extinction only in one patch does not occur for adaptive consumers. Thus, the exclusion of one resource due to apparent competition via shared consumers (Holt, 1977) is not possible because of adaptive consumer behavior. Also, resources in systems with adaptive consumers survive for higher consumer densities when compared with non-adaptive consumers. These results are in line with previous results which treated both resources and consumers as dynamic variables (Colombo and Křivan, 1993; Křivan, 1997,1998; Boukal and Křivan, 1999; van Baalen et al., 2001). These articles showed that adaptive consumer behavior tends to equalize resource levels in both patches and also promotes indefinite coexistence (persistence) of resources in the system when compared with non-adaptive consumers. The case in which consumers are not perfect optimizers, i.e., when the speed of movement between patches is finite was considered by Abrams (2000). Based on numerical simulations he suggested that adaptive consumer behavior does not necessarily decrease spatial resource heterogeneity if consumers are not perfect optimizers. However, Abrams assumed that resource growth is described by a model with the growth rate parameter periodically fluctuating in time, that there was an immigration of resources from an outside pool, and that the rate of consumer movement from patch to patch at a given time was an increasing function of the difference in food intake rates that the consumer would experience in these two patches at that time. Then he examined numerically the dependence of the mean resource densities on the consumer movement rate. The complexity of his model does not allow for analytical treatment and it is difficult to disentangle the effects of various mechanisms contained in the model on the observed increased heterogeneity of resource levels. The effect of gradual switching in similar food webs was studied by van Baalen et al. (2001) and Křivan and Eisner (2003). Their analysis suggests that the qualitative predictions for instantaneous switching also hold for gradual switching provided the switching is fast enough.

Lessells (1995) considered the IFD when resources undergo population dynamics. Her model is based on the assumption that the resource input rates are constant (but they may be different for different patches). Under this assumption there is a stable resource equilibrium and it is easy to show that the Parker's input matching rule holds at this resource equilibrium. My model differs from Lessells model as I do not assume a priori existence of any resource equilibrium. In fact, my model with exponentially increasing resources has no non-trivial equilibrium at all. The difference between my approach and Lessells approach is that my approach allows prediction of non-equilibrium consumer distribution, and the existence of a locally stable equilibrium in my case is an outcome of the model, not an assumption.

I also derived the IFD when two consumers are competing in a two patch environment. To visualize the IFD for two competing species I ploted 0% and 100% isolegs in the consumers phase space (Fig. 5). These isolegs separate consumer species densities for which qualitatively different IFDs are predicted. These results can be compared with those obtained by Křivan and Sirot (2002). For the derivation of isolegs they used the classical Lotka–Volterra competition model for two consumers which considers population dynamics of consumers but it assumes that resources do not undergo population dynamics. They proved that resulting isolegs are piece-wise linear and they cannot be uniquely defined in some regions of the consumer density phase space when interspecific competition is strong compared to intraspecific competition. This is because there exist two possible IFD's in some regions of the consumer density space. In general, when interspecific competition is strong enough the resulting habitat selection map is very complex. On the contrary, the present article is based on a Tilman's type of competition model where resources are depleted by consumers, i.e., they undergo population dynamics. The resulting isolegs are far simpler than those obtained by Křivan and Sirot (2002). Firstly, they are linear, secondly, they are defined for every consumer density. The difference in complexity of isolegs is due to different underlying models. While the Lotka–Volterra competition model predicts multiple equilibria, the resource–two-consumer model predicts only one equilibrium which results in isoleg differences between these two approaches.

Acknowledgments

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Appendix A. The IFD when resources grow exponentially

Here I compute the IFD of the consumer population when resources grow exponentially. The IFD line is described as $\lambda_1 R_1 = \lambda_2 R_2$. Along the IFD line the consumer fitness in both patches equalizes. Vector $n = (\lambda_1, -\lambda_2)$ is perpendicular to the IFD line. Let vector f_1 be the derivative vector $(\frac{dR_1}{dt}, \frac{dR_2}{dt})$ when the first patch is more profitable $(\lambda_1 R_1 > \lambda_2 R_2)$ and hence all the consumers occupy the first patch ($u_1 = 1$ and $u_2 = 0$). Thus, $f_1 = (R_1(r_1 - \lambda_1 C), R_2 r_2)$ denotes the right handside of (1). Vector $f_2 = (R_1 r_1, R_2(r_2 - \lambda_2 C))$ is defined similarly when the second patch is more profitable $(\lambda_1 R_1 < \lambda_2 R_2)$. For $C < \frac{r_1 - r_2}{\lambda_1}$ the scalar product (denoted by $\langle \cdot, \cdot \rangle$) of vectors n and f_1 along the IFD line is positive because $(r_1 > r_2)$

$$\begin{aligned}\langle n, f_1 \rangle &= \lambda_1 R_1 (r_1 - \lambda_1 C) - \lambda_2 r_2 R_2 \\ &= \lambda_1 R_1 (r_1 - r_2) - \lambda_1^2 R_1 C > 0\end{aligned}$$

and

$$\begin{aligned}\langle n, f_2 \rangle &= \lambda_1 r_1 R_1 - \lambda_2 R_2 (r_2 - \lambda_2 C) \\ &= \lambda_1 R_1 (r_1 - r_2) + \lambda_1 \lambda_2 R_1 C > 0.\end{aligned}$$

This implies that trajectories of (1) cross the switching line and all consumers will eventually stay in patch 1. Similarly, for $C > \frac{r_1 - r_2}{\lambda_1}$, $\langle n, f_1 \rangle < 0$ and $\langle n, f_2 \rangle > 0$ which implies that trajectories of model (1) move from both sides to the IFD line and therefore once they reach it they cannot leave it. This allows us to compute controls u_1 and u_2 explicitly. Indeed, as trajectories of (1) move along the IFD then

$$\lambda_1 R_1(t) = \lambda_2 R_2(t). \tag{A.1}$$

Differentiating both sides of this equation gives

$$\lambda_1 \frac{dR_1(t)}{dt} = \lambda_2 \frac{dR_2(t)}{dt}.$$

Substituting the expressions for $\frac{dR_1}{dt}$ and $\frac{dR_2}{dt}$ from model (1) into the above equality gives:

$$\lambda_1 R_1(t)(r_1 - \lambda_1 u_1 C) = \lambda_2 R_2(t)(r_2 - \lambda_2(1 - u_1)C).$$

Because of equality (12) I get

$$\lambda_1 R_1(t)(r_1 - \lambda_1 u_1 C) = \lambda_1 R_1(t)(r_2 - \lambda_2(1 - u_1)C).$$

The solution of the last equation gives expressions (3). Because

$$\langle n, f_2 \rangle = \langle n, f_1 \rangle + (\lambda_1 + \lambda_2)\lambda_1 R_1 C$$

it follows that trajectories of system (1) with adaptive consumers are uniquely defined (Colombo and Křivan, 1993).

Appendix B. The IFD when resources grow logistically

Here I compute the IFD given by u_1 and u_2 for model (7) where resources grow logistically. Following Appendix A, for $\lambda_1 R_1 > \lambda_2 R_2$ $(u_1 = 1, u_2 = 0)$ I denote the vector of right-hand side of Eq. (7) by f_1 and for $\lambda_1 R_1 < \lambda_2 R_2$ $(u_1 = 0, u_2 = 1)$ by f_2, respectively. Along the switching line I have

$$\langle n, f_1 \rangle = R_1 \lambda_1 (r_1 - r_2 - \lambda_1 C) + R_1^2 \lambda_1 \left(\frac{r_2 \lambda_1}{K_2 \lambda_2} - \frac{r_1}{K_1} \right)$$

and

$$\langle n, f_2 \rangle = R_1 \lambda_1 (r_1 - r_2 + \lambda_2 C) + R_1^2 \lambda_1 \left(\frac{r_2 \lambda_1}{K_2 \lambda_2} - \frac{r_1}{K_1} \right).$$

Because

$$\langle n, f_2 \rangle = \langle n, f_1 \rangle + R_1 \lambda_1 C(\lambda_1 + \lambda_2)$$

it follows that trajectories of system (7) are uniquely defined (Colombo and Křivan, 1993). For those points of the IFD line where $\langle n, f_1 \rangle < 0$ and $\langle n, f_2 \rangle > 0$ trajectories are pushed from both sides to the IFD line and, if they reach it, they cannot leave it. This allows us to compute explicitly controls u_1 and u_2 exactly as in the case of exponentially growing resources (Appendix A). Substituting for derivatives expressions from (7) gives

$$u_1 = \frac{r_1 - r_2 + C\lambda_2}{C(\lambda_1 + \lambda_2)} + \frac{R_1(K_1 r_2 \lambda_1 - K_2 r_1 \lambda_2)}{K_1 K_2 C \lambda_2 (\lambda_1 + \lambda_2)}$$

and

$$u_2 = \frac{r_2 - r_1 + C\lambda_1}{C(\lambda_1 + \lambda_2)} - \frac{R_1(K_1 r_2 \lambda_1 - K_2 r_1 \lambda_2)}{K_1 K_2 C \lambda_2 (\lambda_1 + \lambda_2)}.$$

These controls lead to population dynamics along the IFD line which are described by

$$\frac{dR_1}{dt} = R_1 \left(\frac{r_2\lambda_1 + r_1\lambda_2 - \lambda_1\lambda_2 C}{\lambda_1 + \lambda_2} - R_1 \frac{K_1 r_2 \lambda_1^2 + K_2 r_1 \lambda_2^2}{K_1 K_2 \lambda_2 (\lambda_1 + \lambda_2)} \right). \tag{B.1}$$

The corresponding equilibrium is

$$R_1^{\star} = \frac{K_1 K_2 \lambda_2 (r_2\lambda_1 + r_1\lambda_2 - C\lambda_1\lambda_2)}{K_1 r_2 \lambda_1^2 + K_2 r_1 \lambda_2^2}$$

and

$$R_2^{\star} = \frac{K_1 K_2 \lambda_1 (r_2\lambda_1 + r_1\lambda_2 - C\lambda_1\lambda_2)}{K_1 r_2 \lambda_1^2 + K_2 r_1 \lambda_2^2}.$$

At this equilibrium

$$\langle n, f_1 \rangle = \frac{K_1 K_2 r_2 \lambda_1 \lambda_2 (\lambda_1 + \lambda_2)(K_1 \lambda_1^2 C - K_1 \lambda_1 r_1 + K_2 r_1 \lambda_2)(C\lambda_1\lambda_2 - r_2\lambda_1 - r_1\lambda_2)}{(K_1 r_2 \lambda_1^2 + K_2 r_1 \lambda_2^2)^2}$$

and

$$\langle n, f_2 \rangle = \frac{K_1 K_2 r_1 \lambda_1 \lambda_2 (\lambda_1 + \lambda_2)(K_2 \lambda_2^2 C - K_2 \lambda_2 r_2 + K_1 r_2 \lambda_1)(r_2\lambda_1 + r_1\lambda_2 - C\lambda_1\lambda_2)}{(K_1 r_2 \lambda_1^2 + K_2 r_1 \lambda_2^2)^2}.$$

When

$$\frac{r_1\lambda_2 + r_2\lambda_1}{\lambda_1\lambda_2} > C > \frac{r_1(\lambda_1 K_1 - \lambda_2 K_2)}{\lambda_1^2 K_1}$$

then at the equilibrium $\langle n, f_1 \rangle < 0$ and $\langle n, f_2 \rangle > 0$ because of the assumption $K_1\lambda_1 > K_2\lambda_2$. This means that the equilibrium is located in the part of the IFD line where trajectories are pushed from both sides to the line. Consequently, this equilibrium is locally stable. It can also be proved that it is globally stable.

Appendix C. Derivation of isolegs

Here I compute the consumer IFD for model (10). I assume that inequality (11) holds. The corresponding consumer preferences are shown in Fig. 4. There are three "pure" consumer preferences and another two which correspond to the points on the two IFD lines. The dashed IFD line denotes those resource densities at which both patches are equally profitable for species P and the dotted line denotes those resource densities at which both patches are equally profitable for species N. Thus, there are the following five possible consumer distributions over the two patches:

1. All individuals of both species are in patch 1 ($u_1 = v_1 = 1$).
2. All individuals of species N are in patch 2 ($u_1 = 0$) while all individuals of species P are in patch 1 ($v_1 = 1$).
3. All individuals of both species are in patch 2 ($u_1 = v_1 = 0$).
4. Individuals of species N occupy both patches while individuals of species P occupy patch 1 only ($v_1 = 1$).
5. Individuals of species P occupy both patches while individuals of N species occupy patch 2 only ($u_1 = 0$).

The last two distributions under which one species occupies both patches can be computed exactly in the same way as for the case of a single consumer population described in Appendices A and B and I omit details of these calculations. Provided species N is distributed across both patches then the corresponding distribution is given by

$$u_1 = \frac{r_1 r_2 (K_1 \lambda_{N_1} - K_2 \lambda_{N_2}) + r_1 K_2 \lambda_{N_2}^2 N - r_2 K_1 \lambda_{N_1} \lambda_{P_1} P}{(r_2 K_1 \lambda_{N_1}^2 + r_1 K_2 \lambda_{N_2}^2) N}$$

while all individuals of species P are in patch 1 ($v_1 = 1$). Similarly, if species P is distributed over both patches then its distribution is given by

$$v_1 = \frac{r_1 r_2 (K_1 \lambda_{P_1} - K_2 \lambda_{P_2}) + K_2 \lambda_{P_2} (\lambda_{N_2} N + \lambda_{P_2} P)}{(r_2 K_1 \lambda_{P_1}^2 + r_1 K_2 \lambda_{P_2}^2) P}$$

while all individuals of species N are in patch 2 ($u_1 = 0$).

To derive isolegs I will assume that resources are at an equilibrium. For each of the above strategies there is a corresponding resource equilibrium of model (10):

$$E_1 = \left(\frac{K_1}{r_1}(r_1 - \lambda_{N_1} N - \lambda_{P_1} P), K_2 \right),$$

$$E_2 = \left(\frac{K_1}{r_1}(r_1 - \lambda_{P_1} P), \frac{K_2}{r_2}(r_2 - \lambda_{N_2} N) \right),$$

$$E_3 = \left(K_1, \frac{K_2}{r_2}(r_2 - \lambda_{N_2} N - \lambda_{P_2} P) \right)$$

$$E_4 = \left(\frac{K_1 K_2 \lambda_{N_2}(r_2\lambda_{N_1} + \lambda_{N_2} r_1 - \lambda_{N_2}(\lambda_{N_1} N + \lambda_{P_1} P))}{r_2 K_1 \lambda_{N_1}^2 + r_1 K_2 \lambda_{N_2}^2}, \frac{K_1 K_2 \lambda_{N_1}(r_2\lambda_{N_1} + \lambda_{N_2} r_1 - \lambda_{N_2}(\lambda_{N_1} N + \lambda_{P_1} P))}{r_2 K_1 \lambda_{N_1}^2 + r_1 K_2 \lambda_{N_2}^2} \right)$$

$$E_5 = \left(\frac{K_1 K_2 \lambda_{P_2}(r_2\lambda_{P_1} + r_1 \lambda_{P_2} - \lambda_{P_1}(\lambda_{N_2} N + \lambda_{P_2} P))}{r_2 K_1 \lambda_{P_1}^2 + r_1 K_2 \lambda_{P_2}^2}, \frac{K_1 K_2 \lambda_{P_1}(r_2\lambda_{P_1} + r_1 \lambda_{P_2} - \lambda_{P_1}(\lambda_{N_2} N + \lambda_{P_2} P))}{r_2 K_1 \lambda_{P_1}^2 + r_1 K_2 \lambda_{P_2}^2} \right).$$

Now I analyze (with respect to consumer population densities) the position of these equilibria in the resource (R_1, R_2) density space. For example, consider equilibrium E_1. I want to know for which consumer densities this equilibrium belongs to the part of the resource density phase space where optimal consumer distribution is to stay in patch 1 for both consumer species. This happens when fitness computed at the equilibrium is higher for both species in patch 1 than in patch 2, i.e.,

$$\lambda_{P_1} R_1^{\star} > \lambda_{P_2} R_2^{\star},$$

and

$$\lambda_{N_1} R_1^{\star} > \lambda_{N_2} R_2^{\star},$$

where $R_1^{\star}$ and $R_2^{\star}$ are the corresponding resource equilibrial (E_1) densities. However, inequality (11) implies that the second of the two inequalities implies the first inequality. From the second inequality I get that

$$P < I_N^{0\%}(N),$$

where function $I_N^{0\%}$ is defined below. The position of the other four equilibria is then analysed along the same lines. From this analysis I obtain:

- E_1 belongs to the right lower corner of the resource density phase space where consumer distribution is given by $(u_1, v_1) = (1, 1)$ provided $P < I_N^{0\%}$;
- E_2 belongs to the middle part of the resource density space where consumer distribution is given by $(u_1, v_1) = (0, 1)$ provided $I_N^{100\%} < P < I_P^{0\%}$;
- E_3 belongs to the left upper corner of the resource density space where consumer distribution is given by $(u_1, v_1) = (0, 0)$ provided $P < I_N^{100\%}$;
- E_4 belongs to the switching line $(\lambda_{N_1} R_1 = \lambda_{N_2} R_2)$ where consumer distribution is given by $(u_1, v_1) = (u_1^{\star}, 1)$ provided $I_N^{0\%} < P < I_N^{100\%}$;
- E_5 belongs to the switching line $(\lambda_{P_1} R_1 = \lambda_{P_2} R_2)$ where consumer distribution is given by $(u_1, v_1) = (0, v_1^{\star})$ provided $I_P^{0\%} < P$ and $I_N^{100\%} < P$,

where

$$I_N^{0\%} = \frac{r_1(\lambda_{N_1} K_1 - \lambda_{N_2} K_2) - K_1 \lambda_{N_1}^2 N}{\lambda_{P_1} \lambda_{N_1} K_1},$$

$$I_N^{100\%} = \frac{r_1 r_2(\lambda_{N_1} K_1 - \lambda_{N_2} K_2) + r_1 K_2 \lambda_{N_2}^2 N}{r_2 \lambda_{P_1} \lambda_{N_1} K_1},$$

$$I_P^{0\%} = \frac{r_1 r_2(\lambda_{P_1} K_1 - \lambda_{P_2} K_2) + r_1 K_2 \lambda_{N_2} \lambda_{P_2} N}{r_2 \lambda_{P_1}^2 K_1},$$

$$I_N^{100\%} = \frac{r_2(\lambda_{P_2} K_2 - \lambda_{P_1} K_1) - K_2 \lambda_{N_2} \lambda_{P_2} N}{\lambda_{P_2}^2 K_2}.$$

In the quadrangle of consumer density space defined by $\lambda_{N_1} N + \lambda_{P_1} P < r_1$ and $\lambda_{N_2} N + \lambda_{P_2} P < r_2$ where equilibrial resource levels are positive the above four lines given by $P = I_N^{0\%}(N)$, $P = I_N^{100\%}(N)$, $P = I_P^{0\%}(N)$, and $P = I_P^{100\%}(N)$ do not intersect. These lines delimit the regions of the consumer phase space with qualitatively different distributions. The line defined by $P = I_N^{0\%}(N)$ is the 0% isoleg for species N (solid line in Fig. 5), the line $P = I_N^{100\%}(N)$ is the 100% isoleg for species N (long-dashed line in Fig. 5), the line $P = I_P^{0\%}(N)$ is the 0% isoleg for species P (dashed line in Fig. 5), and the line $P = I_P^{100\%}(N)$ is the 100% isoleg for species P (dotted line in Fig. 5). Note that the 0% isoleg for N species exists only provided $\lambda_{N_1}/\lambda_{N_2} > K_2/K_1$ and the 100% isoleg for species P exists only provided $\lambda_{P_1}/\lambda_{P_2} < K_2/K_1$.

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