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A Lyapunov function for piecewise-independent differential equations: stability of the ideal free distribution in two patch environments

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Abstract In this article we construct Lyapunov functions for models described by piecewise-continuous and independent differential equations. Because these models are described by discontinuous differential equations, the theory of Lyapunov functions for smooth dynamical systems is not applicable. Instead, we use a geometrical approach to construct a Lyapunov function. Then we apply the general approach to analyze population dynamics describing exploitative competition of two species in a two-patch environment. We prove that for any biologically meaningful parameter combination the model has a globally stable equilibrium and we analyze this equilibrium with respect to parameters.

Keywords Interspecific competition · Ideal free distribution · Optimal foraging · Isoleg · Differential inclusion · Filippov solution · Lyapunov function · Habitat selection · Resource matching

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1 Introduction

Some models in mathematical biology lead to piecewise-continuous differential equations. These models are described, except along some lower dimensional manifolds, by ordinary differential equations with continuous right-handsides. So called "piecewise-linear models" that describe gene and neural regulatory networks fall in this category [8,12,14,15,18–20,28]. In ecology, piecewise-continuous differential equations arise in models that combine animal behavior with population dynamics [7,9,25,38] or optimal harvesting [29]. Discontinuities enter these models due to sudden switches in the model dynamics. For example, in a gene regulatory network, a gene is off below some switching threshold value of an input signal, and on above that threshold. Likewise, in behavioral ecology, fitness maximization suggests that animals feed on the most abundant resource which leads to "resource switching" as proportions of resources in the environment change [30]. A reasonable definition of a solution for discontinuous differential equations was given by [16]. Filippov definition replaces the original discontinuous differential equation by a differential inclusion that is obtained from the original model by replacing the discontinuous right-handside by an appropriate set-valued map [4,6,16].

Analyzing equilibrium stability for discontinuous differential equations is more complicated when compared with smooth dynamical systems because it uses non-smooth analysis and theory of multivalued functions [5]. A theoretical bifurcation analysis for planar discontinuous systems was given in [16] and [24]. A numerical bifurcation analysis software was also recently developed [13]. Stability of discontinuous systems can be analyzed by a Lyapunov function [4,6,16,37]. However, Lyapunov functions for discontinuous differential equations are typically non-smooth. In fact, [37] provides an example of a non-smooth Lyapunov function for a simple discontinuous differential equation with a globally stable equilibrium for which a smooth Lyapunov function does not exist. General conditions under which a non-smooth Lyapunov functions decreases along trajectories of a discontinuous differential equation are given in [37].

In this article we use a more direct approach to prove global stability of an equilibrium for some models that are described by a piecewise-independent non-linear differential equation. The piecewise-linear models of gene regulatory networks fall in this category. Then we apply our theory to a particular system that was used to describe a competition of two consumer species in a two patch environment [26]. This model extends the Ideal Free Distribution (IFD), originally defined for a single species [17] to two-species environments. The IFD assumes that animals live in discrete patches between which they move freely and instantaneously. They also have a perfect knowledge of the qualities of all patches, and they settle in the patch that 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.

Several attempts to extend the IFD for two or more species can be found in the literature. For example, in a series of articles Rosenzweig [32,33,35] introduced "isolegs", which are the lines in the population-density phase space, that separate regions where qualitatively different habitat preferences are observed (e.g., the first species occupies patch 1 only while the second species occupies both patches etc.). The IFD for multiple species is then graphically visualized by using isolegs. In the literature the shape of isolegs was often assumed to have some a priori chosen functional form [1–3,34,36]. Other authors tried to evaluate the shape of isolegs on the basis of some theoretical arguments [21–23,27,31]. In particular, [27] considered two competing consumer species in a two patch environment and using a game-theoretical approach they defined a corresponding multi-species IFD. Their model was based on the Lotka–Volterra competition model which considers consumer population dynamics but treats resources as fixed. They showed that due to bistability of the underlying model the corresponding IFD may not be uniquely defined provided interspecific competition is strong when compared with intraspecific competition. Using an extension of the evolutionarily stable strategy (ESS) in multispecies environments [10] extended the IFD for two species that either compete for common resources (that do not undergo population dynamics), or are in a predator–prey interaction. [26] considered a reciprocal case where consumer densities are treated as fixed quantities but the resources undergo population dynamics. To derive isolegs, [26] assumed that there exists a globally stable equilibrium for resource dynamics. In this article we analyze this model with respect to parameters and using an appropriate Lyapunov function we show that for any biologically reasonable parameters the model has a globally stable equilibrium.

2 Lyapunov functions for differential inclusions

We consider a system of differential equations

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = f_i(x_1,\dots,x_n), \qquad i = 1,\dots,n \tag{1}$$

with functions f_i that are measurable and locally bounded. Solutions for such differential equations are defined in the Filippov sense [16,6]. Filippov solutions are solutions of the following differential inclusion

$$\frac{\mathrm{d}x}{\mathrm{d}t} \in K(x), \tag{2}$$

where

$$K(x) = \bigcap_{\delta>0} \bigcap_{\mu(N)=0} \overline{\mathrm{co}} f\big(B(x,\delta) \setminus N\big).$$

Here $\overline{co}$ stands for the closed convex hull, $B(x,\delta)$ is the open δ–neighborhood of x, and μ denotes the Lebesgue measure. We remark, that for every initial condition differential inclusion (2) has at least one solution [16]. In general, solutions of model (2) may not be uniquely defined. The right uniqueness of solutions follows if, e. g., K satisfies the one–sided Lipschitz condition [16]. The right uniqueness of solutions implies continuous dependence of solutions of differential inclusion (2) on initial data [16, Corollary 1, p. 89].

A point $E = (E_1, \dots, E_n)$ is an equilibrium of model (2) if it satisfies the following inclusion

$$0 \in K(E).$$

Thus, either the right handside of (1) is continuous at equilibrium E in which case E satisfies the ordinary condition for an equilibrium ($f(E) = 0$), or it is discontinuous in which case the above inclusion must hold. We say that an equilibrium is strictly positive if all its coordinates are positive.

Now we study global asymptotic stability of an equilibrium E of model (1) by using a Lyapunov function. We define $R^n_+ = \{(x_1, \dots, x_n) : x_i \geq 0, \quad \text{for} \quad i = 1, \dots, n\}$, $\text{int}R^n_+ = \{(x_1, \dots, x_n) : x_i > 0, \quad \text{for} \quad i = 1, \dots, n\}$, and $\partial R^n_+ = R^n_+ - \text{int}R^n_+$. For a function $V : R^n \mapsto R$ and a positive number a we define

$$B(V, a) = \{(x_1, \dots, x_n) \in R^n : V(x_1, \dots, x_n) < a\},$$

and

$$S(V, a) = \{(x_1, \dots, x_n) \in R^n : V(x_1, \dots, x_n) = a\}.$$

In what follows we assume that R^n_+ is invariant for differential equation (1). The set of all ω limit points that can be reached from $\text{int}R^n_+$ is denoted by Ω_{int} (i.e., there exists a solution $x(t)$ of (1) and a sequence of times t_k, $t_k \to \infty$ such that $x(t_k) > 0$, i.e., $x_i(t_k) > 0$ for every $i = 1, \dots, n$, and $\lim_{n\to\infty} x(t_n) = x$).

"Natural" Lyapunov functions for discontinuous differential equations often lack differentiability [16]. For locally Lipschitz Lyapunov functions generalized derivatives based on the Clark's gradient can be used [16,37]. Here we give a definition of a Lyapunov function which assumes continuity only.

Definition 1 *Function $V : R^n \mapsto R$ is a Lyapunov function if it satisfies the following conditions*:

(i) *V is a continuous, non-negative function*
(ii) *$V(x) \to \infty$ when $\|x\| \to \infty$*
(iii) *There exists a unique point E such that $V(E) = 0$*
(iv) *For every $a > 0$, every solution of (1) starting from $S(V, a) \cap \text{int}R^n_+$ enters $B(V, a)$ for a small positive time interval.*

The next theorem is a slight modification of standard stability theorems for differential equations with discontinuous right-handsides [16,37]. First, it does not assume any sort of differentiability of the Lyapunov function, second, it predicts stability with respect to a given set (here with respect to $\text{int}R^n_+$).

Theorem 1 *Let an equilibrium E of model (1) be strictly positive. Let a Lyapunov function V be given,* $\Omega_{\text{int}} \cap \partial R_+^n = \emptyset$, *and* ∂R_+^n *be an invariant set. Then the equilibrium E is globally asymptotically stable in* $\text{int}R_+^n$.

Proof First, we prove that equilibrium E is stable. Let $\eta > 0$ and $m_\eta = \inf\{V(x) : \|x-E\| = \eta\}$. Due to our assumptions (i) and (iii) on function V, we have $m_\eta > 0$. Let $\delta > 0$ be such that $\{x : \|x - E\| < \delta\} \subset R_+^n$ and $V(x) < m_\eta$ for $\|x - E\| < \delta$. If $x(t)$ is a solution of (1) such that $\|x(0) - E\| < \delta$, then $V(x(0)) < m_\eta$ and because V decreases along solutions of (1), $V(x(t)) < m_\eta$ for all $t > 0$. It follows that $\|x(t) - E\| < \eta$ for all $t > 0$.

Second, we prove asymptotic stability. Let $\tilde{x}(t)$ be a solution of (1) such that $\tilde{x}(0) \in S(V, a_1) \cap \text{int}R_+^n$ for some $a_1 > 0$. Let $l(t) = V(\tilde{x}(t))$. Due to (iv) $l(t)$ is decreasing and $L = \lim_{t\to\infty} l(t) = 0$. Indeed, if $L > 0$ then an ω-limit point $\mathcal{O} \in \Omega_{\text{int}}$ exists. Due to the assumption $\Omega_{\text{int}} \cap \partial R_+^n = \emptyset$ point $\mathcal{O}$ belongs to $S(V, L) \cap \text{int}R_+^n$. Thus, there exists a sequence $t_n \to \infty$ such that $\tilde{x}(t_n) \to \mathcal{O}$. Let $x_n(t)$ be solutions of (1) such that $x_n(0) = \tilde{x}(t_n)$. Due to Lemma 1 on page 87 in [16] there exists a subsequence which converges to a solution $x(t)$ of model (1). Because $x(0) = \mathcal{O}$ and this solution enters $B(V, L)$ for some $t > 0$, it follows that some of the functions $x_n(t)$ must also enter $B(V, L)$, which is a contradiction with the definition of L. Since E is a unique point in $B(V, a_1)$ for which $V = 0$, the solution $\tilde{x}(t)$ converges to E. The global asymptotic stability of E is proved.

In what follows we will assume that functions f_i are discontinuous along a discontinuity manifold M that is given by a function $h : R_+^{n-1} \mapsto R$,

$$M = \{(x_1, \ldots, x_n) : x_n = h(x_1, \ldots, x_{n-1})\},$$

and for $x^0 \in M$ we define (we assume that the limits below exist)

$$f_-(x^0) = \lim_{x \nearrow x^0} f(x), \quad f_+(x^0) = \lim_{x \searrow x^0} f(x).$$

Let γ be an orthogonal vector to M at point $x^0 \in M$, i.e.,

$$\gamma = \left(-\frac{\partial h}{\partial x_1}, \ldots, -\frac{\partial h}{\partial x_{n-1}}, 1\right).$$

At the points of the discontinuity manifold M where solutions cannot leave it (such part of the discontinuity manifold is called the sliding regime and the points satisfy $\langle f_-(x^0), \gamma\rangle > 0$ and $\langle f_+(x^0), \gamma\rangle < 0$ where $\langle \cdot, \cdot\rangle$ stands for the usual scalar product) the right hand-side of (2) can be replaced by the "Filippov field"

$$f_F(x^0) = \mu(x^0) f_+(x^0) + (1 - \mu(x^0)) f_-(x^0) = \frac{\langle f_-(x^0), \gamma\rangle\, f_+(x^0) - \langle f_+(x^0), \gamma\rangle\, f_-(x^0)}{\langle f_-(x^0) - f_+(x^0), \gamma\rangle},$$

where

$$\mu(x^0) = \frac{-\langle f_-(x^0), \gamma\rangle}{\langle f_+(x^0) - f_-(x^0), \gamma\rangle}, \tag{3}$$

Filippov [16]. The Filippov vector field f_F is obtained as the intersection of the tangent plane to M with the line segment that connects the two adjacent vector fields f_+ and f_-.

Filippov [16, p. 156] showed that if the Lyapunov function decreases everywhere except the discontinuity manifold (which is a set of zero measure), the corresponding equilibrium may not be stable, because trajectories can diverge from the equilibrium along the discontinuity manifolds. This causes a problem how to define a "derivative" of the Lyapunov function at the discontinuity manifolds, because at these points the Lyapunov function is often non differentiable. [37] proved that the derivative of a regular (e.g., a pointwise maximum of smooth functions) function V along solutions of model (2) satisfies for almost all times t

$$\frac{\mathrm{d}V(x(t))}{\mathrm{d}t} \in DV(x(t)),$$

where

$$\mathrm{D}V(x(t)) = \bigcap_{\xi\in\partial V(x(t))} \langle \xi, K(x(t))\rangle,$$

∂V denotes the Clarke's generalized gradient. If E is an equilibrium of model (2), V is a non-negative function that attains its minimum at E, and $DV(x) \leq 0$ then V is a Lyapunov function and the equilibrium is stable. However, computation of DV can be quite complicated task.

2.1 A Lyapunov function for piecewise-independent differential inclusions

In this article we assume that model (1) is described by a piecewise-independent differential equation

$$\frac{\mathrm{d}x_i}{\mathrm{d}t} = f_i(x_i), \qquad i = 1, \ldots, n \tag{4}$$

and that the discontinuities form a linear manifold. In this case we define

$$V(x_1, \ldots, x_n) = \max_{0\leq i\leq n} c_i|x_i - E_i|, \tag{5}$$

where c_i is a positive constant, and E is an equilibrium.

Remark 1 Conditions of Definition 1 are easily verified for the Lyapunov function given by (5). If the point x^0 belongs to $S(V, a)$ then there exists an index set $\{i_1, \ldots, i_k\}$ such that

$$x^0_{i_\ell} = (-1)^{\varepsilon_{i_\ell}} \frac{a}{c_{i_\ell}} + E_{i_\ell}, \qquad \ell = 1, \ldots, k$$

where ε_i is 0 or 1. If x^0 is a point of continuity of function f then for V to be a Lyapunov function we require

$$(-1)^{\varepsilon_{i_1}} f_{i_1}(x^0_{i_1}) < 0, \ldots, (-1)^{\varepsilon_{l_k}} f_{i_k}(x^0_{i_k}) < 0.$$

If the point x^0 lies on the discontinuity manifold then there are two possibilities: (1) It is in the sliding regime and then vector f is replaced by the Filippov vector field f_F; (2) It is not in the sliding regime (in which case trajectories of (2) pass transversally through the discontinuity manifold) and then we require the above inequalities hold for both f_+ and f_-. We show how to apply Theorem 1 to analyze a particular system that arises in ecology.

3 The IFD of two competing species

Here we consider a model of competition of two species N and P in an environment consisting of two foraging patches [26]. We assume that consumers do not undergo population dynamics while resources are exploited by consumers. The resource dynamics are described by the following model

$$\begin{aligned} \frac{\mathrm{d}R_1}{\mathrm{d}t} &= r_1 R_1 \left(1 - \tfrac{R_1}{K_1}\right) - \lambda_{N_1} u_1 N R_1 - \lambda_{P_1} v_1 P R_1, \\ \frac{\mathrm{d}R_2}{\mathrm{d}t} &= r_2 R_2 \left(1 - \tfrac{R_2}{K_2}\right) - \lambda_{N_2} u_2 N R_2 - \lambda_{P_2} v_2 P R_2. \end{aligned} \tag{6}$$

Here, R_i is density of resources in patch i $(= 1, 2)$, N and P are (fixed) overall abundances of the two competing populations, r_i is the per capita instantaneous resource growth rate, $\lambda_{N_i}, \lambda_{P_i}$ are the resource cropping rates, K_i is the resource environmental carrying capacity, and u_i (v_i) is the portion of individuals N (P) in patch i. Because we assume that travel time between patches is negligible we have $u_1 + u_2 = v_1 + v_2 = 1, u_i \geq 0, v_i \geq 0$. The functions $u_i(t), v_i(t)$ are chosen so that the consumer fitness defined as

$$W_N = \lambda_{N_1} u_1 R_1 + \lambda_{N_2} u_2 R_2, \quad W_P = \lambda_{P_1} v_1 R_1 + \lambda_{P_2} v_2 R_2$$

maximizes at every time instant. Thus, the average food intake rate is taken here as a proxy for Darwinian fitness. Fitness maximization gives the following optimal strategy:

- If $\lambda_{N_1} R_1 - \lambda_{N_2} R_2 > 0$ then $u_1 = 1$,
- If $\lambda_{P_1} R_1 - \lambda_{P_2} R_2 > 0$ then $v_1 = 1$,
- If $\lambda_{N_1} R_1 - \lambda_{N_2} R_2 < 0$ then $u_1 = 0$,
- If $\lambda_{P_1} R_1 - \lambda_{P_2} R_2 < 0$ then $v_1 = 0$,

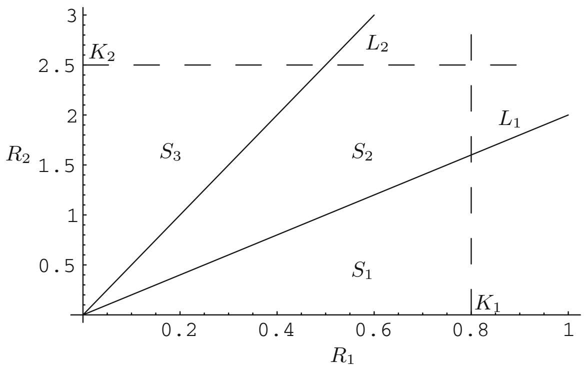

Fig. 1 Position of sectors S_1, S_2 and S_3 in the resource 1—resource 2 density phase space provided inequality (7) holds. Model (6) is discontinuous along lines L_1 and L_2

- If $\lambda_{N_1} R_1 - \lambda_{N_2} R_2 = 0$ then W_N is constant and u_i is not uniquely defined $(0 \le u_i \le 1)$,
- If $\lambda_{P_1} R_1 - \lambda_{P_2} R_2 = 0$ then W_P is constant and v_i is not uniquely defined $(0 \le v_i \le 1)$.

By L_i we denote the half lines

$$L_1 = \left\{ (R_1, R_2) : R_1 \ge 0, R_2 = \frac{\lambda_{N_1}}{\lambda_{N_2}} R_1 \right\};\ L_2 = \left\{ (R_1, R_2) : R_1 \ge 0, R_2 = \frac{\lambda_{P_1}}{\lambda_{P_2}} R_1 \right\}$$

that separate three sectors in the resource density phase space:

$$\begin{aligned} S_1 &= \left\{ (R_1, R_2) : 0 \le R_1,\ \ 0 \le R_2 < \frac{\lambda_{N_1}}{\lambda_{N_2}} R_1 \right\}, \\ S_2 &= \left\{ (R_1, R_2) : 0 \le R_1,\ \ \frac{\lambda_{N_1}}{\lambda_{N_2}} R_1 < R_2 < \frac{\lambda_{P_1}}{\lambda_{P_2}} R_1 \right\}, \\ S_3 &= \left\{ (R_1, R_2) : 0 \le R_1,\ \ \frac{\lambda_{P_1}}{\lambda_{P_2}} R_1 < R_2 \right\}. \end{aligned}$$

Without loss of generality we will assume that

$$\frac{\lambda_{N_1}}{\lambda_{N_2}} < \frac{\lambda_{P_1}}{\lambda_{P_2}}, \tag{7}$$

see Fig. 1. The right hand side of model (6) in these sectors will be denoted by (f_i, g_i), $(i = 1, 2, 3)$. In particular, in sector S_1

$$\begin{aligned} f_1(R_1, R_2) &= r_1 R_1 (1 - R_1/K_1) - \lambda_{N_1} N R_1 - \lambda_{P_1} P R_1, \\ g_1(R_1, R_2) &= r_2 R_2 (1 - R_2/K_2), \end{aligned}$$

in sector S_2

$$f_2(R_1,R_2) = r_1R_1(1 - R_1/K_1) - \lambda_{P_1}PR_1,$$
$$g_2(R_1,R_2) = r_2R_2(1 - R_2/K_2) - \lambda_{N_2}NR_2,$$

and in sector S_3

$$f_3(R_1,R_2) = r_1R_1(1 - R_1/K_1),$$
$$g_3(R_1,R_2) = r_2R_2(1 - R_2/K_2) - \lambda_{N_2}NR_2 - \lambda_{P_2}PR_2.$$

Thus, this model falls into the category of piecewise-independent equations, because in all these sectors the two resource population dynamics are decoupled. We remark that model (6) is multivalued along lines L_i ($i = 1,2$) and it coincides with the Filippov regularization of the discontinuous system defined on sectors S_1, S_2 and S_3. We study resource dynamics along the lines L_i now. In principle there are three possibilities. Either trajectories cross L_i transversally, or they move along L_i for some positive time, or they are not uniquely defined. First, we study trajectories that start from a point on line L_1. By $\mathcal{M}$ we denote the set of points on L_1 in which the sliding regime occurs ($\mathcal{M}$ is also called the sliding domain). The sliding regime is governed by the Filippov system [16]

$$\begin{aligned}\frac{\mathrm{d}R_1}{\mathrm{d}t} &= f_F(R_1,R_2) = \mu(R_1)f_1(R_1,R_2) + (1 - \mu(R_1))f_2(R_1,R_2),\\ \frac{\mathrm{d}R_2}{\mathrm{d}t} &= g_F(R_1,R_2) = \mu(R_1)g_1(R_1,R_2) + (1 - \mu(R_1))g_2(R_1,R_2),\end{aligned} \tag{8}$$

where

$$\mu(R_1) = \frac{\left(\frac{\lambda_{N_1}r_2}{\lambda_{N_2}K_2} - \frac{r_1}{K_1}\right)R_1 + r_1 - r_2 + \lambda_{N_2}N - \lambda_{P_1}P}{(\lambda_{N_1} + \lambda_{N_2})N} \tag{9}$$

is between zero and one.

Remark 2 Let $\gamma = (-\lambda_{N_1}, \lambda_{N_2})$ be an orthogonal vector to L_1. Because along the line L_1, $\langle (f_1,g_1),\gamma\rangle - \langle (f_2,g_2),\gamma\rangle = \lambda_{N_1}(\lambda_{N_1} + \lambda_{N_2})NR_1 > 0$ we get

$$\langle (f_1,g_1),\gamma\rangle > \langle (f_2,g_2),\gamma\rangle. \tag{10}$$

There are just two possibilities: Either solutions of model (6) cross the line from one side to the other, or solutions move along the line in "sliding motion". The regime in which trajectories along L_1 are not unique (i.e., $\langle (f_1,g_1),\gamma\rangle < 0$ and $\langle (f_2,g_2),\gamma\rangle > 0$) is not possible. The sliding regime takes place if and only if $0 \le \mu \le 1$. Indeed, if the sliding regime occurs, than $\langle (f_1,g_1),\gamma\rangle \ge 0$ and $\langle (f_2,g_2),\gamma\rangle \le 0$ and one of these expressions is nonzero. From (3) (where we set $f_+ = (f_1, g_1)$ and $f_- = (f_2, g_2)$) it follows that $0 \leq \mu \leq 1$. On the contrary, if $0 \leq \mu \leq 1$ then

$$\langle (f_1, g_1), \gamma \rangle = \frac{(\mu - 1)\langle (f_2, g_2), \gamma \rangle}{\mu}.$$

This means that the signs of $\langle (f_i, g_i), \gamma \rangle$ $(i = 1, 2)$ are different and $\langle (f_1, g_1), \gamma \rangle \geq 0$ and $\langle (f_2, g_2), \gamma \rangle \leq 0$ because of (10).

Model (8) has an equilibrium

$$D = (D_1, D_2) = \left(\frac{K_1 K_2 \lambda_{N_2} (r_2 \lambda_{N_1} + \lambda_{N_2} r_1 - \lambda_{N_2} (\lambda_{N_1} N + \lambda_{P_1} P))}{r_2 K_1 \lambda_{N_1}^2 + r_1 K_2 \lambda_{N_2}^2}, \frac{\lambda_{N_2}}{\lambda_{N_1}} D_1 \right) \tag{11}$$

if

$$P < \frac{\lambda_{N_2} r_1 + \lambda_{N_1} r_2 - \lambda_{N_1} \lambda_{N_2} N}{\lambda_{N_2} \lambda_{P_1}}$$

and $0 \leq \mu(D_1) \leq 1$. In this case the equilibrium is positive. Equilibrium D is asymptotically stable in L_1 because

$$\frac{\mathrm{d} f_F(D)}{\mathrm{d} R_1} = -\frac{D_1}{\lambda_{N_1} + \lambda_{N_2}} \frac{\lambda_{N_2}^2 r_1 K_2 + \lambda_{N_1}^2 r_2 K_1}{\lambda_{N_2} K_1 K_2} < 0 \tag{12}$$

whenever the equilibrium exists. However, this does not imply that D is asymptotically stable in the resource density phase space.

A similar situation holds along the discontinuity line L_2 in which case the resource population dynamics in the sliding regime are governed by the following system

$$\begin{aligned} \frac{\mathrm{d} R_1}{\mathrm{d} t} &= f_F(R_1, R_2) = \nu(R_1) f_3(R_1, R_2) + (1 - \nu(R_1)) f_2(R_1, R_2), \\ \frac{\mathrm{d} R_2}{\mathrm{d} t} &= g_F(R_1, R_2) = \nu(R_1) g_3(R_1, R_2) + (1 - \nu(R_1)) g_2(R_1, R_2), \end{aligned} \tag{13}$$

where

$$\nu(R_1) = \frac{\left(\frac{r_1}{K_1} - \frac{\lambda_{P_1} r_2}{\lambda_{P_2} K_2} \right) R_1 + r_2 - r_1 + \lambda_{P_1} P - \lambda_{N_2} N}{(\lambda_{P_1} + \lambda_{P_2}) P} \tag{14}$$

is between zero and one. The corresponding equilibrium is

$$F = (F_1, F_2) = \left(\frac{K_1 K_2 \lambda_{P_2} (r_2 \lambda_{P_1} + r_1 \lambda_{P_2} - \lambda_{P_1} (\lambda_{N_2} N + \lambda_{P_2} P))}{r_2 K_1 \lambda_{P_1}^2 + r_1 K_2 \lambda_{P_2}^2}, \lambda_{P_1} / \lambda_{P_2} F_1 \right). \tag{15}$$

This equilibrium is positive when

$$P < \frac{\lambda_{P_2} r_1 + \lambda_{P_1} r_2 - \lambda_{N_2}\lambda_{P_1} N}{\lambda_{P_2}\lambda_{P_1}}$$

and $0 \le \nu(F_1) \le 1$. Equilibrium F is also asymptotically stable in L_2 whenever it exists because

$$\frac{\mathrm{d}f_F(F)}{\mathrm{d}R_1} = -\frac{F_1}{\lambda_{P_1} + \lambda_{P_2}} \frac{\lambda_{P_2}^2 r_1 K_2 + \lambda_{P_1}^2 r_2 K_1}{\lambda_{P_2} K_1 K_2} < 0.$$

Isolegs for the two consumer species are the lines in the consumer density phase space (N, P) that separate regions where qualitatively different habitat preferences are predicted [27,31–33,35]. In particular, the 100% (0%) isoleg separates the part of the consumer density phase space where all individuals of the given species occupy the second (first) patch from the rest of the phase space. There are four such isolegs [26]:

$$\begin{aligned}
I_N^{100\%}(N) &= \frac{r_1 r_2(\lambda_{N_1} K_1 - \lambda_{N_2} K_2) + r_1 K_2 \lambda_{N_2}^2 N}{r_2 \lambda_{P_1}\lambda_{N_1} K_1},\\
I_P^{0\%}(N) &= \frac{r_1 r_2(\lambda_{P_1} K_1 - \lambda_{P_2} K_2) + r_1 K_2 \lambda_{N_2}\lambda_{P_2} N}{r_2 \lambda_{P_1}^2 K_1},\\
I_N^{0\%}(N) &= \frac{r_1(\lambda_{N_1} K_1 - \lambda_{N_2} K_2) - K_1 \lambda_{N_1}^2 N}{\lambda_{P_1}\lambda_{N_1} K_1},\\
I_P^{100\%}(N) &= \frac{r_2(\lambda_{P_2} K_2 - \lambda_{P_1} K_1) - K_2 \lambda_{N_2}\lambda_{P_2} N}{\lambda_{P_2}^2 K_2}.
\end{aligned}$$

The isolegs are shown in Fig. 2 as the thick lines. The thick solid line is the 0% isoleg for species N, the long-dashed line is the 100% isoleg for the same species. Similarly, the short-dashed line is the 0% isoleg for species P and dot-line is the 100% isoleg for the same species.

Qualitative behavior of model (6) depends on the position of the following points:

$$\begin{aligned}
A &= (A_1, A_2) = \left(K_1\left(1 - \frac{\lambda_{P_1} P}{r_1}\right), K_2\left(1 - \frac{\lambda_{N_2} N}{r_2}\right)\right),\\
\tilde{B} &= (B_1, K_2) = \left(K_1\left(1 - \frac{\lambda_{N_1} N + \lambda_{P_1} P}{r_1}\right), K_2\right),\\
B &= (B_1, 0) = \left(K_1\left(1 - \frac{\lambda_{N_1} N + \lambda_{P_1} P}{r_1}\right), 0\right),
\end{aligned}$$

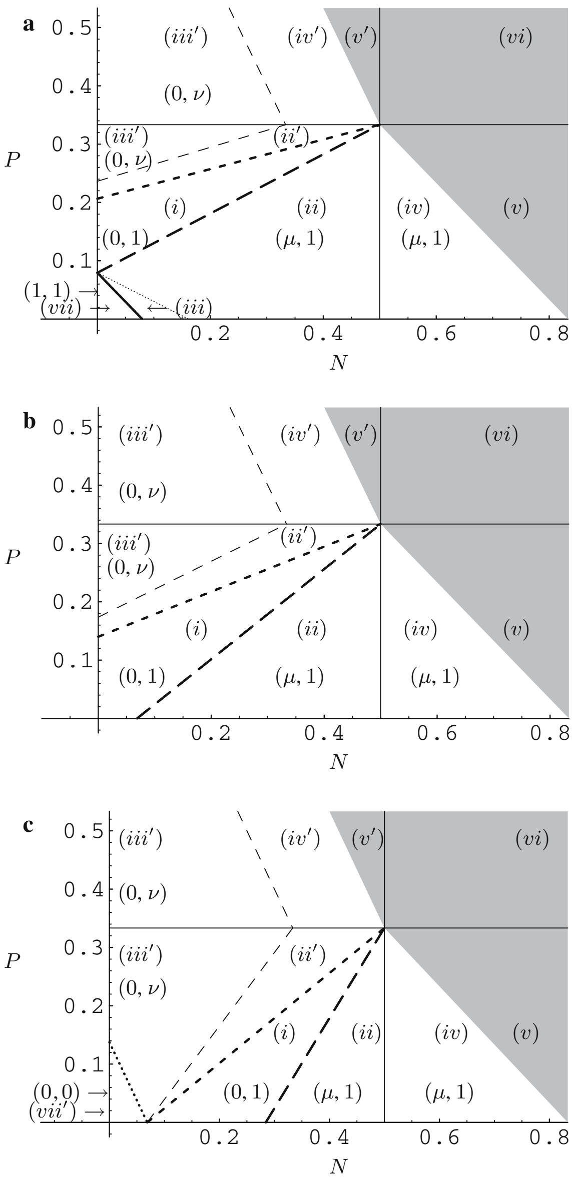

Fig. 2 This figure analysis resource equilibrial densities (for definition of qualitative cases (i), …,(vii′) see text) and consumer spatial distribution (shown as pairs of numbers) as function of consumer densities *N* and *P*. The *thick lines* are isolegs (*solid line* is the 0% isoleg for species *N*, the *long-dashed line* is the 100% isoleg for species *N*, the *short-dashed line* is the 0% isoleg for species *P* and *dot-line* is the 100% isoleg for the same species). The *gray region* shows consumer densities for which both resources are depleted. In (**a**) the first patch is better for both species at low densities ($\lambda_{P_1}/\lambda_{P_2} > \lambda_{N_1}/\lambda_{N_2} > K_2/K_1$, $K_1 = 35$, $K_2 = 20$), in (**b**) the first patch is better for species *P* and the second patch is better for species *N* when at low densities ($\lambda_{P_1}/\lambda_{P_2} > K_2/K_1 > \lambda_{N_1}/\lambda_{N_2}$, $K_1 = 23$, $K_2 = 10$) and in (**c**) the second patch is better for both species at low densities ($K_2/K_1 > \lambda_{P_1}/\lambda_{P_2} > \lambda_{N_1}/\lambda_{N_2}$, $K_1 = 23$, $K_2 = 40$). Other parameters: $\lambda_{N_1} = 0.3$, $\lambda_{N_2} = 0.4$, $\lambda_{P_1} = 0.3$, $\lambda_{P_2} = 0.2$, $r_1 = 0.1$, $r_2 = 0.2$

$$C = (0, C_2) = \left(0, K_2\left(1 - \frac{\lambda_{N_2}N + \lambda_{P_2}P}{r_2}\right)\right),$$

$$\tilde{C} = (K_1, C_2) = \left(K_1, K_2\left(1 - \frac{\lambda_{N_2}N + \lambda_{P_2}P}{r_2}\right)\right).$$

We remark, that points A, B, $\tilde{B}$, C and $\tilde{C}$ are equilibria of model (6) provided they belong to the adequate sectors (i.e., $A \in S_2$, $B, \tilde{B} \in S_1$, $C, \tilde{C} \in S_3$). If this is not so then we call the point a "virtual equilibrium" (e.g., $A \in S_1$). Position of

these equilibria with respect to the two consumer densities can be analyzed by using isolegs.
Using Lyapunov functions given by (5) we will analyze existence and stability of equilibria with respect to consumer densities.

(i) We assume that A is an equilibrium of model (6), i.e., $A \in S_2$ (Fig. 3a) which happens for consumer densities satisfying

$$I_N^{100\%}(N) < P < I_P^{0\%}(N) \tag{16}$$

(see the region denoted by (i) in Fig. 2). The above inequalities immediately imply that species N occupies patch 2 while species P occupies patch 1 (which is indicated by distribution $(0, 1)$ in Fig. 2 where the first number is the proportion of species N in patch 1 and the second number is the proportion of species P in patch 1). Let

$$V(R_1, R_2) = \max\left(\frac{|R_1 - A_1|}{A_1}, \frac{|R_2 - A_2|}{A_2}\right). \tag{17}$$

The following proposition is proved in Appendix A.

Proposition 1 *Point $A \in S_2$ is a globally asymptotically stable equilibrium of model* (6) *in* $\text{int}R_+^2$. *Function V defined by* (17) *is a corresponding Lyapunov function.*

The following three cases lead to the Lyapunov function given in Proposition 2.

(ii) We assume that A is a virtual equilibrium which belongs to sector S_1 and $A_2 > \lambda_{N_1}/\lambda_{N_2} B_1$ (Fig. 3b). In the consumer density phase space this means that

$$I_N^{0\%}(N) < \frac{r_1 r_2 (K_1 \lambda_{N_1} - K_2 \lambda_{N_2}) + (\lambda_{N_2}^2 r_1 K_2 - \lambda_{N_1}^2 r_2 K_1) N}{K_1 r_2 \lambda_{N_1} \lambda_{P_1}} < P < I_N^{100\%}(N)$$

and

$$N \leq \frac{r_2}{\lambda_{N_2}}$$

(see region (ii) in Fig. 2a, where the thin dotted line is given by the expression in the first of the two above formulas). This immediately implies that the first consumer species occupies both patches. We observe that $P > I_N^{0\%}(N)$ is equivalent with $K_2 > \lambda_{N_1}/\lambda_{N_2} B_1$ which implies that $\tilde{B}$ is either in sector S_2 or S_3. Trajectories starting in sector S_2 are driven toward the virtual equilibrium A which is in sector S_1 and trajectories that start in sector S_1 are driven to virtual equilibrium $\tilde{B}$ which is either in S_2 or S_3. Thus, $\tilde{A} = (\lambda_{N_2}/\lambda_{N_1} A_2, A_2)$ is a point in the sliding domain $(0 < \mu < 1)$ and solutions of the Filippov system (8) move at the point $\tilde{A}$ along line L_1 in the direction away from the origin ($g_F(\tilde{A}) > 0$ because $f_1(\tilde{A}) < 0, g_1(\tilde{A}) > 0, f_2(\tilde{A}) > 0, g_2(\tilde{A}) = 0$).

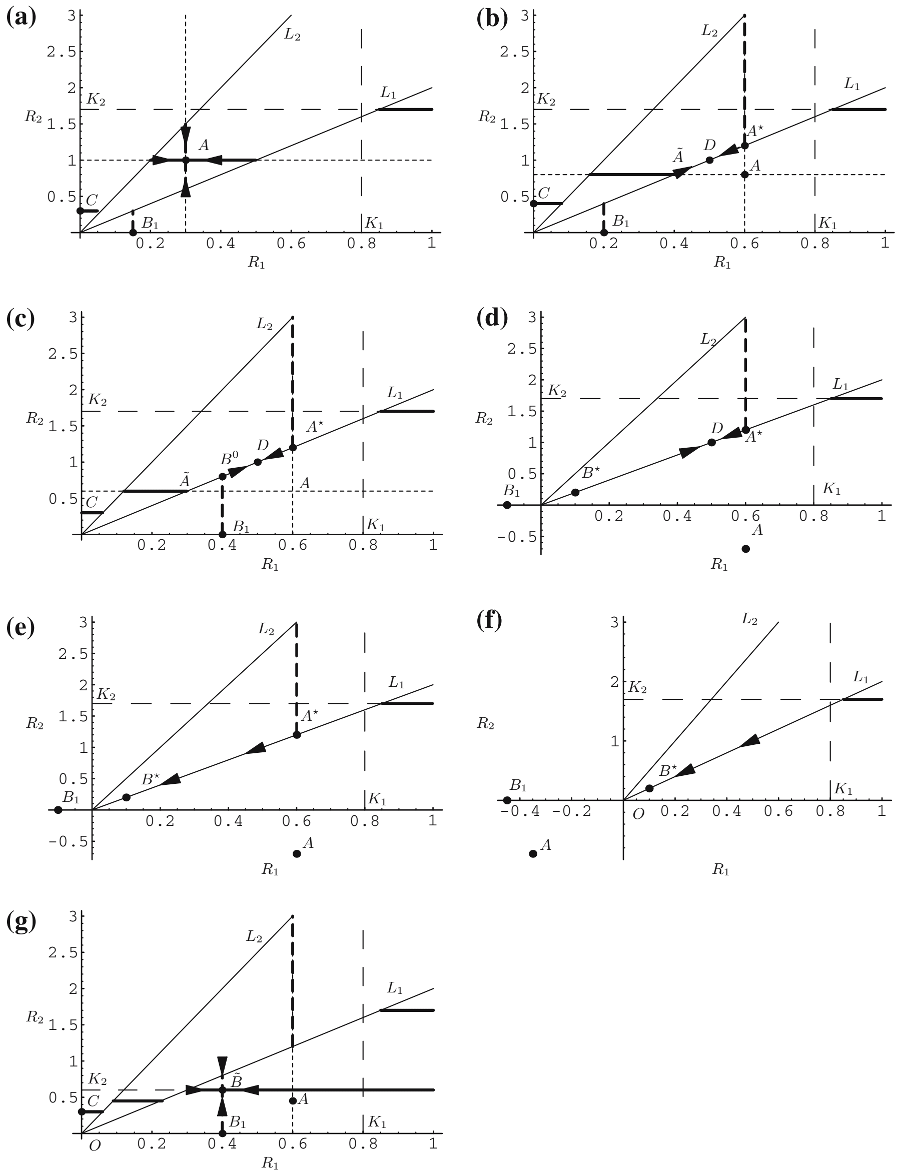

Fig. 3 Qualitatively different positions of equilibria A, B and C of model (6). Panels (**a**)–(**g**) correspond to cases (**i**)–(**vii**) discussed in text and shown in Fig. 2

Let

$$A^\star = \begin{cases} \left(A_1, \frac{\lambda_{N_1}}{\lambda_{N_2}} A_1\right) & \text{if } \frac{\lambda_{N_1}}{\lambda_{N_2}} A_1 < K_2, \\ \left(\frac{\lambda_{N_2}}{\lambda_{N_1}} K_2, K_2\right) & \text{if } \frac{\lambda_{N_1}}{\lambda_{N_2}} A_1 > K_2. \end{cases}$$

Since $A_2 > \lambda_{N_1}/\lambda_{N_2}B_1$, we have $B_1 < \tilde{A}_1 < A_1^\star$. Because either $f_1(A^\star) < 0$, $g_1(A^\star) > 0, f_2(A^\star) = 0, g_2(A^\star) < 0$ in which case $f_F(A^\star) < 0$, or $f_1(A^\star) < 0$, $g_1(A^\star) = 0, f_2(A^\star) > 0, g_2(A^\star) < 0$ in which case $g_F(A^\star) < 0$, the Filippov field at $A^\star$ points toward the origin. It follows that there exists a locally attractive equilibrium D of the Filippov field in L_1 ($B_1 < \tilde{A}_1 < D_1 < A_1^\star \le A_1$). Due to the linearity of $\mu(R_1)$ in R_1 we know that there is just one such point and it is given by (11). The point D is between $\tilde{A}$ and $A^\star$.

(iii) Third, we assume that $B_1 > 0, A_1 > 0$, $K_2 > \lambda_{N_1}/\lambda_{N_2}B_1$ and $A_2 \le \lambda_{N_1}/\lambda_{N_2}B_1$ (Fig. 3c) (we remark that from definition of points A and B it follows that $B_1 < A_1$). In the consumer density phase space this corresponds to the case where

$$I_N^{0\%} < P < \frac{r_1 r_2(K_1\lambda_{N_1} - K_2\lambda_{N_2}) + (\lambda_{N_2}^2 r_1 K_2 - \lambda_{N_1}^2 r_2 K_1)N}{K_1 r_2 \lambda_{N_1}\lambda_{P_1}}, \quad P \le \frac{r_1}{\lambda_{P_1}},$$

see Fig. 2a. Similarly to the previous case the above inequalities imply that the first consumer N occupies both patches. Let us consider point $B^0 = (B_1, \lambda_{N_1}/\lambda_{N_2}B_1)$ which is on L_1. We have $f_1(B^0) = 0, g_1(B^0) > 0, f_2(B^0) > 0, g_2(B^0) < 0$, see Fig. 3c. Point B^0 is in the region of the sliding regime where the Filippov field points in the direction away from the origin. Because the Filippov field at the point $A^\star$ points toward the origin there exists an equilibrium D of the Filippov regularization (8) on the line L_1 ($B_1 < D_1 < A_1^\star \le A_1$) and it is given again by formula (11).

The point D is between B^0 and $A^\star$.

(iv) We assume that $B_1 \le 0, A_1 > 0, A_2 \le 0$,

$$P < \frac{\lambda_{N_2} r_1 + \lambda_{N_1} r_2 - \lambda_{N_1}\lambda_{N_2} N}{\lambda_{N_2}\lambda_{P_1}}.$$

The right hand side of the above inequality is the line separating regions denoted as (vi) and (v) in Fig. 2.

In this case we consider $B^\star = (\varepsilon, \lambda_{N_1}/\lambda_{N_2}\varepsilon)$ (Fig. 3d) where ε is a small positive number such that the R_1 component of the Filippov field

$$f_F = \frac{R_1}{\lambda_{N_1} + \lambda_{N_2}}\left(\lambda_{N_2} r_1 + \lambda_{N_1} r_2 - \lambda_{N_2}\lambda_{P_1}P - \lambda_{N_1}\lambda_{N_2}N - \left(\frac{r_1}{K_1}\lambda_{N_2}^2 + \frac{r_2}{K_2}\lambda_{N_1}^2\right)\frac{R_1}{\lambda_{N_2}}\right) \tag{18}$$

evaluated at $B^\star$ is positive, i.e.,

$$f_F(B^\star) > 0. \tag{19}$$

We have $f_1(B^\star) < 0, g_1(B^\star) > 0, f_2(B^\star) > 0, g_2(B^\star) < 0$. The point $B^\star$ is on L_1 and it is a point of the sliding regime (Remark 2) at which trajectories move along L_1 in the direction away from the origin due to inequality (19).

Because the Filippov field at the point $A^\star$ points toward the origin as we have already shown, there is an interval with the sliding regime (Remark 2) and there exists an equilibrium D (see (11)) of the Filippov field on the line L_1. The point D is between 0 and $A^\star$.

So far we have proved that under condition (ii)–(iv) the sliding regime occurs along the segment of the line L_1 with the end-points

$$T_1 = (Q_1, \lambda_{N_1}/\lambda_{N_2} Q_1), \qquad T_2 = (Q_2, \lambda_{N_1}/\lambda_{N_2} Q_2), \tag{20}$$

where

$$Q_1 = \max\left\{0, (r_2 - r_1 - \lambda_{N_2} N + \lambda_{P_1} P)\left(\frac{\lambda_{N_1} r_2}{\lambda_{N_2} K_2} - \frac{r_1}{K_1}\right)^{-1}\right\}$$
$$Q_2 = \max\left\{0, (r_2 - r_1 + \lambda_{N_1} N + \lambda_{P_1} P)\left(\frac{\lambda_{N_1} r_2}{\lambda_{N_2} K_2} - \frac{r_1}{K_1}\right)^{-1}\right\}.$$

Moreover, the equilibrium D of model (6) belongs to the sliding regime. At this equilibrium, species N occupies both patches while species P occupies only patch 1. The set of consumer densities under which this distribution at the resource equilibrium exists corresponds to species distributions denoted as $(\mu, 1)$ in Fig. 2. The boundary of this set is formed by isolegs $I_N^{100\%}$ (long-dashed line), $I_N^{0\%}$ (solid line) and the extinction line (which is the boundary of the gray area). The exact distribution of the N species at the equilibrium is given by formula (9). The next proposition, which is proved in Appendix A, shows that this equilibrium is globally asymptotically stable.

Proposition 2 *Under one of the assumptions* (ii)–(iv) *equilibrium D, given by formula* (11)*, is globally asymptotically stable in* $\mathrm{int}R_+^2$.

Function

$$V(R_1, R_2) = \max\left(\frac{|R_1 - D_1|}{D_1}, \frac{|R_2 - D_2|}{D_2}\right) \tag{21}$$

is a corresponding Lyapunov function.

Now we will treat two cases that lead to the extinction of both resources.

(v) We assume that $B_1 \leq 0, A_1 > 0, A_2 \leq 0$,

$$P \geq \frac{\lambda_{N_2} r_1 + \lambda_{N_1} r_2 - \lambda_{N_1} \lambda_{N_2} N}{\lambda_{N_2} \lambda_{P_1}},$$

in Fig. 3e. We observe that the Filippov vector field evaluated at $B^\star$ and $A^\star$ points toward origin. Because $B^\star$ is arbitrarily close to the origin and the Filippov vector field is linear in μ it follows that the sliding regime operates along the segment of L_1 between the origin and $A^\star$. Along this segment trajectories move toward the origin.

(vi) We assume that A belongs to the third quadrant ($A_1 < 0, A_2 < 0$; Fig. 3f) which corresponds to consumer densities that satisfy

$$N > \frac{r_2}{\lambda_{N_2}}, \quad P > \frac{r_1}{\lambda_{P_1}}.$$

The following Proposition is proved in Appendix A.

Proposition 3 *If* (v) *or* (vi) *hold then the origin is globally asymptotically stable in* R^2_+. *Function*

$$V(R_1, R_2) = \max(\lambda_{N_1}|R_1|, \lambda_{N_2}|R_2|) \tag{22}$$

is the corresponding Lyapunov function.

The set of consumer densities that correspond to cases (v) and (vi) is shaded in Fig. 2. As both species go extinct, it does not make any sense to speak about their distribution at the equilibrium.

(vii) We consider the remaining case where $\tilde{B}$ is an equilibrium of model (6), which means that it is in S_1. Moreover, we assume that A belongs either to S_1 (Fig. 3g), or to the fourth quadrant ($A_1 > 0, A_2 < 0$). The following Proposition is proved in Appendix A.

Proposition 4 *Let* (vii) *be fulfilled. Then the point* $\tilde{B}$ *is globally asymptotically stable equilibrium in* $\text{int}R^2_+$. *The corresponding Lyapunov function is*

$$V(R_1, R_2) = \max\left(\frac{|R_1 - \tilde{B}_1|}{\tilde{B}_1}, \frac{|R_2 - \tilde{B}_2|}{\tilde{B}_2}\right). \tag{23}$$

Thus, in case (vii) both species occupy the more profitable patch 1 at the resource equilibrium (Fig. 2a). The boundary of this region in the consumer density phase space is formed by the isoleg $I_N^{0\%}$.

We summarize our results.

Theorem 2 *Let us assume that* $\lambda_{N_1}/\lambda_{N_2} \leq \lambda_{P_1}/\lambda_{P_2}$. *Then model* (6) *has the following globally asymptotically stable equilibria:*

1. *A is globally asymptotically stable in* $\text{int}R^2_+$ *if assumption* (i) *holds.*
2. *D given by* (11), *which is in the sliding domain with end-points* T_1, T_2, *is globally asymptotically stable in* $\text{int}R^2_+$ *if one of the conditions* (ii)–(iv) *holds.*
3. 0 *is globally asymptotically stable in* R^2_+ *if* (v) *or* (vi) *holds.*
4. $\tilde{B}$ (*which is in sector* S_1) *is globally asymptotically stable in* $\text{int}R^2_+$ *if* (vii) *holds.*

Appendix B shows that conditions (i)–(vii) cover all relevant possibilities except the case where A belongs to S_3, or the second quadrant. In these cases we proceed in an analogous way. We define symmetric cases (see Fig. 2):

(i′) This case is identical to (i),
(ii′) $A_1 \geq \lambda_{P_2}/\lambda_{P_1} C_2, A \in S_3$,
(iii′) $C_2 > 0, A_1 \leq \lambda_{P_2}/\lambda_{P_1} C_2, A_2 > 0, K_1 > \lambda_{P_2}/\lambda_{P_1} C_2$,
(iv′) $C_2 \leq 0, A_1 \leq 0, A_2 > 0$ and

$$P < \frac{\lambda_{P_2} r_1 + \lambda_{P_1} r_2 - \lambda_{N_2} \lambda_{P_1} N}{\lambda_{P_1} \lambda_{P_2}},$$

(v′) $C_2 \leq 0, A_1 \leq 0, A_2 > 0$ and

$$P \geq \frac{\lambda_{P_2} r_1 + \lambda_{P_1} r_2 - \lambda_{N_2} \lambda_{P_1} N}{\lambda_{P_1} \lambda_{P_2}},$$

(vi′) This case is identical to the case (vi),
(vii′) $\tilde{C} \in S_3$ where

$$\tilde{C} = \left(K_1, K_2 \left(1 - \frac{\lambda_{N_2} N + \lambda_{P_2} P}{r_2} \right) \right).$$

The corresponding equilibrium in the sliding regime along L_2 is then F (given by formula (15)), instead of D.

Theorem 3 *Let $\lambda_{N_1}/\lambda_{N_2} \leq \lambda_{P_1}/\lambda_{P_2}$. If assumptions* (ii′), …, (iv′) *hold then F is a globally asymptotically stable in* intR^2_+ *equilibrium of model* (1) *which is in the sliding domain of L_2. If* (v′) *holds then the origin is globally asymptotically stable in R^2_+. If* (vii′) *holds then point $\tilde{C}$ which is in the sector S_3 is globally asymptotically stable in* intR^2_+.

The proof is analogous to the proof of Theorem 1.

4 Discussion

Lyapunov functions for differential equations with discontinuous right-hand-side are often only Lipschitz continuous, non-differentiable functions. In fact, [37] gave an example of a system for which any Lyapunov function must be non-differentiable. Lyapunov theory for such systems was developed using Clarke's generalized gradients [16,37]. However, verifying the condition under which the corresponding Lyapunov function along trajectories is decreasing can be quite difficult for non-trivial problems. In this article we used a simpler geometrical approach that can be applied in some fairly simple problems that arise in biology. This approach is based on a particular choice of a Lyapunov function for which it is easy to verify that it decreases along trajectories of a differential equation. Our approach can be useful in those applications that lead to differential equations which are piecewise-independent. Such models arise in description of gene and neural networks [8,12,14,15,18,28] in optimal harvesting problems [29], and in population dynamics [26].

Using this approach we have completely analyzed a model of two competing species in a two patch environment that was introduced in [26]. This model assumes adaptive animal dispersal between two patches which leads to population dynamics that are described by piecewise-independent nonlinear differential equations. Using a Lyapunov function we validated analytically predictions of numerical simulations given in [26] which suggested that a single, globally asymptotically stable equilibrium exists for all biologically relevant parameter values. Moreover, we analyzed the position of the equilibrium as a function of all parameters of the model.

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A Appendix

Here we prove Theorem 1.

First, we prove that functions V given in Propositions 1, …,4 (cases (i)–(vii)) are Lyapunov functions for model (6).

Case (i). For a positive number a the level set $V(R_1, R_2) = a$ (with V given by (17)) is a rectangle with sides

$$s_1(a) = \left\{(R_1, R_2) : R_2 < A_2, \frac{|R_1 - A_1|}{A_1} \le a, \ \frac{|R_2 - A_2|}{A_2} = a\right\},$$

$$s_2(a) = \left\{(R_1, R_2) : R_1 > A_1, \frac{|R_1 - A_1|}{A_1} = a, \ \frac{|R_2 - A_2|}{A_2} \le a\right\},$$

$$s_3(a) = \left\{(R_1, R_2) : R_2 > A_2, \frac{|R_1 - A_1|}{A_1} \le a, \ \frac{|R_2 - A_2|}{A_2} = a\right\},$$

$$s_4(a) = \left\{(R_1, R_2) : R_1 < A_1, \frac{|R_1 - A_1|}{A_1} = a, \ \frac{|R_2 - A_2|}{A_2} \le a\right\}.$$

The lower boundary of the rectangle $s_1(a)$ is either completely in the first quadrant (Fig. 4a), or it is disjoint with the first quadrant (Fig. 4b). Let us assume that $s_1(a) \subset \text{int}R^2_+$ (Fig. 4a). Then $g_2(R_1, R_2)/R_2 = r_2(1 - R_2/K_2) - \lambda_{N_2} N > 0$ along the side $s_1(a)$ in sector S_2 because $A \in S_2$ is an equilibrium of model (6) ($g_2(A_1, A_2) = 0$), function g_2/R_2 is a decreasing function of R_2 in sector S_2, and $R_2 < A_2$ along $s_1(a)$. Similarly, $g_1(s_1(a)) > 0$ in sector S_1 (because $g_1(s_1(a)) > g_2(s_1(a)) > 0$). Due to the construction of level sets, $s_1(a)$ is a subset of sectors S_1 and S_2 only. Let $L_1 \cap s_1(a) = U$. Then either U belongs to the

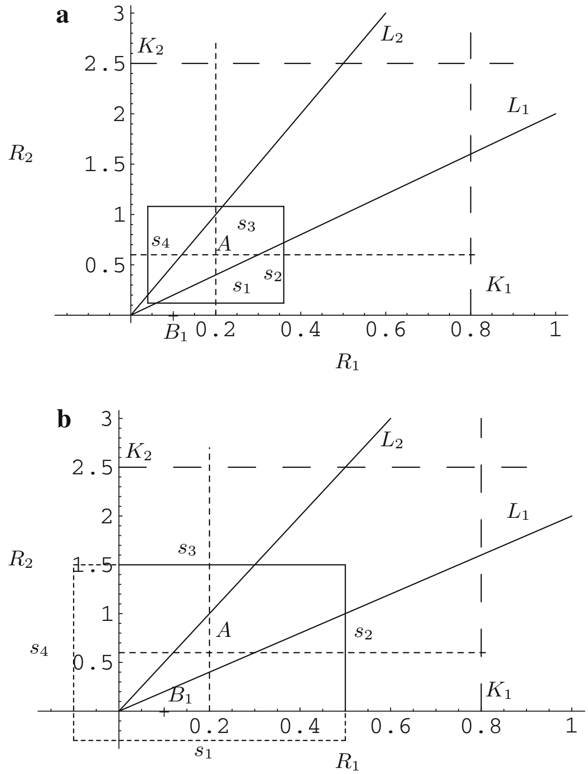

Fig. 4 This figure shows the position of the sides $s_1(a), \ldots, s_4(a)$ of the level set $V(R_1, R_2) = a$. Panel A (B) shows the case where side s_1 is subset of (disjoint with) the first quadrant

sliding regime $\mathcal{M}$ in which case we have that the Filippov vector field $g_F(U) > 0$ (as $g_1(U) > g_2(U) > 0$), or U is not in the sliding regime in which case we have $g_2(U) > 0$. We have proved that solutions starting from points on the lower boundary $s_1(a)$ of the level set enter the interior of the rectangle $V = a$ with the possible exception of end-points.

Now let us consider the part of the second side $s_2(a)$ which is in the first quadrant. This side is in sectors S_1 and S_2 (Fig. 4). Points on $s_2(a)$ fulfill $R_1 > A_1 > B_1$ and because $f_2(A_1, A_2) = 0$ and f_2/R_1 decreases in R_1, $f_2(s_2(a)) < 0$ on S_2. As $f_1(s_2(a)) < f_2(s_2(a))$ we get that also $f_1(s_2(a)) < 0$ on S_1. These inequalities imply that even if (R_1, R_2) is in the sliding regime of L_1 (i.e., $(R_1, R_2) \in L_1 \cap \mathcal{M}$) we have $f_F(R_1, R_2) < 0$. If L_1 intersects with the lower right corner of the rectangle (i.e., $s_1(a) \cap s_2(a) \cap L_1 = \{V\}$), then the inequalities $g_1(V) > g_2(V) > 0, f_1(V) < f_2(V) < 0$ imply that the lower left corner of the rectangle cannot be in the sliding regime $\mathcal{M}$. We conclude that solutions that start from $s_2(a)$ also enter the rectangle. The proof that solutions starting from sides $s_3(a)$ and $s_4(a)$ enter the interior of the rectangle follows the same lines and we omit it here. Since we considered all sides $s_1(a), \ldots, s_4(a)$ the solutions starting from end-points of the sides enter the considered rectangle as well. Thus, if a solution reaches at some moment τ the boundary of the rectangle (i.e., $V(R_1(\tau), R_2(\tau)) = a$ for some $a > 0$) then it enters the interior of this rectangle, i.e., $V(R_1(t), R_2(t)) < a$ for $\tau < t < \tau + \delta$ and sufficiently small δ. We have proved that V is a Lyapunov function according to Definition 1.

If $s_1(a)$ is disjoint with the first quadrant (Fig. 4b) then we consider rectangle bounded by $s_1(a)$, $s_2(a)$, and ∂R^n_+ (i.e., the rectangle is in R^2_+). In this case trajectories of the model cannot leave this rectangle because ∂R^n_+ is invariant and the above analysis along sides $s_2(a)$ and $s_3(a)$ holds also in this case.

Now, we shall deal with cases (ii), …(iv). The function V is defined as in Proposition 2. From analysis of cases (ii), …,(iv) we know that $B_1 < D_1 < A_1^\star \leq A_1$ in cases (ii), (iii), and $0 < D_1 < A_1^\star \leq A_1$ in case (iv). We can proceed as follows. If the side $s_1(a)$ is in the first quadrant then due to our definition of the function V it is completely in the sector S_1 and $g_1(R_1, R_2) > 0$ (because the side is below the line $R_2 = K_2$). On the part of $s_2(a)$ which is completely in sector S_1 we have $f_1(R_1, R_2) < 0$ because $B_1 < R_1$ there. On $s_3(a)$ which is in the first quadrant we have $g_2(R_1, R_2) < 0$ for $(R_1, R_2) \in S_2$ and $g_3(R_1, R_2) < 0$ on S_3 since $D_2 > \tilde{A}_2 = A_2$. Finally, on the part of $s_4(a)$ in first quadrant we have $f_2(R_1, R_2) > 0$ on S_2 and $f_3(R_1, R_2) > 0$ on S_3 since this side is left from D and $D_1 < A_1 < K_1$. To complete the proof we have to consider point $(Z_1, Z_2) = (D_1(1 + a), D_2(1 + a))$. If this point belongs to the sliding domain $\mathcal{M}$ then the solution starting at this point tends to the point D which follows immediately from the analysis of the cases (ii)–(iv). If this point does no belong to $\mathcal{M}$ then the solution starting from this point crosses L_1 transversally. Assume that the solution leaves S_1 and enters S_2. It means that for some small positive t the solution will be in S_2 but there is $g_2 < 0$ such that the solution must enter the rectangle. Similar reasoning is valid for points

$$(Z_1, Z_2) = (D_1(1 - a), D_2(1 - a)).$$

Case (v) (Proposition 3). We remark, that for Lyapunov function (22), the level set $V(R_1, R_2) = a$ is the part of the R^2 plane bounded from the right by

$$s_2(a) = \{(R_1, R_2) : R_1 = a/\lambda_{N_1}, R_2 \leq a/\lambda_{N_2}\},$$

and from above by

$$s_3(a) = \{(R_1, R_2) : R_2 = a/\lambda_{N_2}, R_1 \leq a/\lambda_{N_1}\}.$$

As $B_1 \leq 0$ it follows that $\lambda_{N_1} N + \lambda_{P_1} P \geq r_1$ and

$$\frac{f_1}{R_1} = r_1 \left(1 - \frac{R_1}{K1}\right) - \lambda_{N_1} N - \lambda_{P_1} P < 0$$

in S_1. Since we assume $A_2 = K_2(1 - \lambda_{N_2} N / r_2) \leq 0$, we get that

$$\frac{g_2}{R_2} = r_2 \left(1 - \frac{R_2}{K2}\right) - \lambda_{N_2} N < 0$$

in S_2. In sector S_3 we have $g_3/R_2 \le g_2/R_2 < 0$ which implies that V defined by (22) is the Lyapunov function.

Case (vi) (Proposition 3). Since we assume $\lambda_{N_2}N > r_2$ and $\lambda_{P_1}P > r_1$ we have $f_1/R_1 = r_1(1 - R_1/K_1) - \lambda_{N_1}N - \lambda_{P_1}P < -r_1R_1/K_1 - \lambda_{N_1}N < 0$ in S_1, $g_2/R_2 = r_2(1 - R_2/K_2) - \lambda_{N_2}N < -r_2R_2/K_2 < 0$ in S_2, and $g_3/R_2 = r_2(1 - R_2/K_2) - \lambda_{N_2}N - \lambda_{P_2}P < g_2/R_2 < 0$ in S_3. Once again, V defined by (22) is the Lyapunov function.

Case (vii) (Proposition 4). The Lyapunov function is given as in case (i) (see (17)). We remark that the lower side $s_1(a)$ of the rectangle is in S_1. Because $R_2 < K_2$ along $s_1(a)$, we get $g_1(s_1(a)) > 0$. Similarly, the right side $s_2(a)$ of the rectangle is in S_1. Because $R_1 > B_1$ along $s_2(a)$ we have $f_1(s_2(a)) < 0$. Along the part of $s_3(a)$ that is in S_1 we have $g_1(s_3(a)) < 0$ as $R_2 > K_2$, along the part of $s_3(a)$ that is either in S_2 or S_3 we have $g_3(s_3(a)) < g_2(s_3(a)) < g_1(s_3(a)) < 0$. Similarly, $f_1(s_4(a)) > 0$ in S_1 since $R_1 < B_1$ there, $f_2(s_4(a)) > f_1(s_4(a)) > 0$ in S_2 and finally $f_3(s_4(a)) > 0$ since $R_1 < K_1$.

Second, it remains to prove that points from Ω_{int} do not belong to ∂R^n_+ in cases (i), ...,(iv), and (vii) (Theorem 1). Such points could be only the origin, B, and C. In these cases we use Lyapunov functions given by (17) and the equilibria $A, D, \tilde{B}$ are strictly positive. First we show that $0 \notin \Omega_{int}$. Let us consider $B(V, V(0))$ (we have $V(0) = 1$) which contains the region $\{(R_1, R_2) : 0 < R_i < \varepsilon,\ \ i = 1, 2\}$ for a small positive ε. Let us assume that there exists a sequence of $t_n, t_n \to \infty, \tilde{x}(t_n) \to 0, \tilde{x}_i(t_n) > 0$. For sufficiently large t_n the points $\tilde{x}(t_n)$ will be in $B(V, V(0))$ which means that $V(\tilde{x}(t_n)) < V(0)$. Since the function $V(\tilde{x}(t))$ is decreasing, we get a contradiction with the assumption that $\tilde{x}(t_n) \to 0$. Point B is excluded by the fact that $g_1(R_1, R_2) > 0$ close to this point in the first open quadrant. Similarly, point C is excluded because $f_3(R_1, R_2) > 0$ in the first open quadrant. Applying Theorem 1, assertions 1,2, and 4 of Theorem 2 are proved.

Now we prove assertion 3 of Theorem 2, i.e., we consider cases (v), (vi) for which the corresponding Lyapunov function is given by (22). Let $\tilde{x}(t)$ be a solution of model (6) starting from $R^2_+ \setminus 0$. It follows that functions $\tilde{x}_1(t), \tilde{x}_2(t)$ are strictly decreasing at every point in $R^2_+ \setminus 0$. Since 0 is a unique point fulfilling $V(0) = 0$, all solutions converge monotonically to the origin (we remark that points B, C are outside of R^2_+ which implies global asymptotic stability of the origin).

B Appendix

Here we show that if $A \in S_1 \cup S_2 \cup \{(R_1, R_2) : R_1 > 0, R_2 < 0\}$, then conditions (i), ...,(vii) cover all possibilities.

Condition (ii) can be rewritten:

$$\text{(ii)} : A_1 > 0, A_2 > 0, A_2 > \lambda_{N_1}/\lambda_{N_2}B_1, A_2 < \lambda_{N_1}/\lambda_{N_2}A_1.$$

The complement can be expressed:

$$(\alpha) : A_1 \le 0, \text{ or } (\beta) : A_1 > 0, A_2 \le 0, \text{ or } (\gamma) : A_1 > 0, A_2 > 0, A_2 \le \lambda_{N_1}/\lambda_{N_2}B_1,$$

$$\text{or } (\delta): A_1 > 0, A_2 > 0, A_2 > \lambda_{N_1}/\lambda_{N_2} B_1, A_2 \geq \lambda_{N_1}/\lambda_{N_2} A_1.$$

In the case (γ) we have $B_1 > 0$, in the case (δ) the condition $A_2 > \lambda_{N_1}/\lambda_{N_2} B_1$ is superfluous since $A_1 > B_1$.

Case (α) is covered by (vi) and if $A \in \{(R_1, R_2) : R_1 < 0, 0 < R_2\}$ then we use Theorem 2. Case (β) is covered by $(iv) + (v)$ $(B_1 \leq 0, A_1 > 0, A_2 \leq 0)$ for $B_1 \leq 0$ and by $(iii) + (vii)$ $(B_1 > 0, A_1 > 0, A_2 < \lambda_{N_1}/\lambda_{N_2} B_1)$ for $B_1 > 0$. Case (γ) is covered by (iii)+(vii) (B_1 has to be positive). Case (δ) is covered by (i) and if A is in the third quadrant then we use Theorem 2.

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