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Interim Report IR-05-083

Border Collision Bifurcations in the Evolution of Mutualistic Interactions

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Approved by

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Contents

BORDER COLLISION BIFURCATIONS IN THE EVOLUTION OF MUTUALISTIC INTERACTIONS

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The paper describes the slow evolution of two adaptive traits that regulate the interactions between two mutualistic populations (e.g. a flowering plant and its insect pollinator). For frozen values of the traits, the two populations can either coexist or go extinct. The values of the traits for which populations extinction is guaranteed are therefore of no interest from an evolutionary point of view. In other words, the evolutionary dynamics must be studied only in a viable subset of trait space, which is bounded due to the physiological cost of extreme trait values. Thus, evolutionary dynamics experience so-called border collision bifurcations, when a system invariant in trait space hits the border of the viable subset. The unfolding of standard and border collision bifurcations with respect to two parameters of biological interest is presented. The algebraic and boundary-value problems characterizing the border collision bifurcations are described together with some details concerning their computation.

Keywords: Adaptive dynamics; border collision bifurcations; continuation techniques; evolution; mutualism; population dynamics.

1. Introduction

Border collision bifurcations have been originally defined for n-dimensional continuous piecewise smooth maps depending on parameters [Feigin, 1970, 1974, 1978; Nusse & Yorke, 1992, 1995; Nusse *et al.*, 1994]. In the simplest case, there is a $(n-1)$-dimensional manifold on which the map is not differentiable. Such a manifold is the boundary (border) of two open nonoverlapping regions of state space in which the map is smooth. When a parameter is varied, a border collision bifurcation occurs if a fixed (or periodic) point hits the border.

Border collision bifurcations also arise in discontinuous piecewise smooth vector fields, called Filippov systems [Filippov, 1964, 1988], where relationships among state variables are smooth but can be of different nature in different regions of state space. In fact, in such systems the flow is continuous and a periodic orbit may graze the border separating two regions for critical values of the parameters. Under suitable conditions, such a bifurcation corresponds to a border collision bifurcation in the Poincaré map associated with the periodic orbit [Bernardo di *et al.*, 1999].

More abstractly, border collision bifurcations can be seen in any n-dimensional dynamical system characterized by some sort of irregularity when the system state reaches a $(n-1)$-dimensional manifold, namely the *border*. According to this definition, the collision of a system invariant with the border, when a parameter is varied, is called a *border collision bifurcation*.

Thus, border collision bifurcations occur also in switched systems (which include continuous piecewise smooth maps, see e.g. [Liberzon, 2003]), and in impact systems (see e.g. [Brogliato, 1999, Chap. 7]), described by smooth vector fields whose orbits undergo abrupt jumps in state space when the border is reached. Finally, there are smooth dynamical systems in which orbits are only defined in a bounded subset of state space, because the system is destroyed when the border is reached. In order to guarantee the sustainability of such systems, it is therefore necessary that no attractor hits the border when parameters are varied.

Obviously, the consequences of a border collision bifurcation on the system behavior strongly depend on the considered class of systems. However, the detection and continuation of the bifurcation in parameter space poses the same problems.

Though many recent theoretical results on border collision bifurcations are available for piecewise smooth systems (see e.g. [Feigin, 1994, 1995; Bernardo di *et al.*, 1999, 2001, 2002; Kuznetsov *et al.*, 2003]) and impact systems (see, e.g. [Nordmark, 1991; Chin *et al.*, 1994; Foale, 1994; Foale & Bishop, 1994]), and many applications in several areas of engineering and applied sciences (ranging from power electronics, vibro-impacting mechanics and automatic control to earthquake engineering, natural resources management and ecology) have been developed (resp. [Bernardo di *et al.*, 1998; Mc Geer, 1990; Utkin, 1977; Hogan, 1989; Dercole *et al.*, 2003; Křivan & Sikder, 1999], just to mention a few), less attention has been paid to systems defined in bounded subsets of state space.

The aim of this paper is to present the unfolding of standard and border collision bifurcations in a second-order continuous-time system defined in a bounded subset of state space. The system describes the slow evolution by natural selection of the adaptive traits of two interacting populations.

Evolutionary change of an adaptive trait is brought about when a slightly different mutant conspecific (with a slightly different trait) appears in a resident population, invades (i.e. gives rise to a growing population), and wins the competition against the resident population, thus replacing the former resident trait. Repeated invasions and replacements result in the evolutionary dynamics of the trait [Darwin, 1859]. Thus, evolutionary dynamics occur on a much longer timescale than that of individuals' births, interactions, and deaths, which determine the dynamics of population abundances. Therefore, by a timescale separation argument, on a short timescale, adaptive traits can be seen as frozen parameters of the ecological model which describes the dynamics of population abundances. For frozen values of the traits, the populations can either coexist on a strictly positive attractor of the ecological model or some of them can go extinct. Thus, only trait values for which the ecological model has a strictly positive attractor are of interest, since otherwise populations extinction is guaranteed in the short-term. In other words, the evolutionary dynamics are defined in a viable subset of trait space, which is bounded due to the physiological cost of extreme trait values. This is why natural evolution is "at risk": if the evolutionary orbit reaches the border of the viable subset, some of the coevolving populations disappear (*evolutionary extinction* or *suicide* [Matsuda & Abrams, 1994; Ferrière, 2000]).

The specific application considered in this paper addresses the evolution of mutually beneficial interactions between two different species (e.g. a flowering plant and its insect pollinator) as described in [Ferrière *et al.*, 2002], where a partial bifurcation analysis has been carried out without, however, taking border collision bifurcations into account. The evolution of two adaptive traits regulating the rates of commodities provision (e.g. a reward like nectar or a service like pollination) is given by two smooth ODEs defined on a bounded viable subset of the two-dimensional trait space. The border of the viable subset corresponds to the evolutionary suicide of both populations.

The paper is organized as follows. In Sec. 2 the ecological model and the evolutionary model are developed and a brief biological background is given. Section 3 presents the unfolding of standard and border collision bifurcations with respect to two parameters of biological interest, together with the algebraic and boundary-value problems characterizing the border collision bifurcations, while some computational details are reported in Appendix. The biological implications of the obtained bifurcation scenario and a comment on the relevance of border collision bifurcations close the paper.

As for the style of the paper, I have taken the liberty of being somehow naïve in the presentation of the model and in the biological interpretation of the results, as well as in the description of the mathematical technicalities. I hope that this will make the paper accessible to a broader class of readers, ranging from theoretical biologists to applied mathematicians.

2. The Ecological and Evolutionary Models

A longstanding puzzle posed by mutually beneficial interactions between two different species (*interspecific mutualism*) is their persistence in spite of apparent evolutionary nonsustainability. Interspecific mutualism inherently exhibits conflicts of interest between the interacting species in that selection should favor "cheating" individuals that reap mutualistic benefits while providing fewer commodities to the partner species [Axelrod & Hamilton, 1981; Soberon Mainero & Martinez del Rio, 1985; Bull & Rice, 1991; Addicott, 1996]. Thus, cheating should gradually erode the mutualistic interaction, leading to dissolution or reciprocal extinction [Roberts & Sherratt, 1998; Doebeli & Knowlton, 1998]. However, recent empirical findings indicate that associations of mutualists and cheaters have existed over long evolutionary periods [Machado *et al.*, 1996; Pellmyr *et al.*, 1996; Pellmyr & Leebens-Mack, 1999; Després & Jaeger, 1999; Bronstein, 2001].

Despite the widespread occurrence and obvious importance of mutualistic interactions, the theory of mutualistic coevolution is virtually nonexistent (but see [Kiester *et al.*, 1984; Law, 1985; Frank, 1994, 1996; Law & Dieckmann, 1997; Doebeli & Dieckmann, 2000] and, in particular [Ferrière *et al.*, 2002]).

Ferrière *et al.* [2002] offered a general explanation for the evolutionary origin of cheaters and the surprising sustainability of mutualistic associations by assuming a competitive premium for "good mutualists" that provide large amounts of commodities. Provided commodities represent a limited resource for the partner species, therefore there is intraspecific competition for commodities [Addicott, 1985; Iwasa *et al.*, 1995; Bultman *et al.*, 2000], and competition in nature is, as a rule, asymmetrical [Brooks & Dodson, 1965; Lawton & Hassell, 1981; Karban, 1986; Callaway & Walker, 1997] (i.e. cheaters or good mutualists are better competitors). Clearly, if any competitive asymmetry were to give advantage to cheaters, there would be no way to sustain the mutualistic interactions. However, individuals often discriminate among partners according to the quantity of rewards they provide and associate differentially with higher reward producers [Bull & Rice, 1991; Christensen *et al.*, 1991; Mitchell, 1994; Anstett *et al.*, 1998]. Thus, a competitive advantage to good mutualists may explain a richer range of evolutionary outcomes.

Ferrière *et al.* [2002] analyzed the case of a two-species obligate mutualism (i.e. both species cannot survive without the partner's support; see [Doebeli & Dieckmann, 2000] for the nonobligate case) and assumed that each species has a continuous adaptive trait that measures the rate at which commodities are provided to the partner. Thus, low (high) trait values correspond to cheaters (good mutualists). Provision of commodities is costly in terms of reproduction or survival, and cheaters incur a reduced cost [Boucher *et al.*, 1992; Maynard Smith & Szathmary, 1995; Herre *et al.*, 1999; Bronstein, 2001].

The evolutionary model describing the dynamics of the two traits is developed following the approach of *adaptive dynamics theory* [Dieckmann & Law, 1996; Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998]. This approach is based on the assumption that small and rare random mutations are followed by natural selection, so that the dynamics of the traits can be described in a purely deterministic way, through a system of ODEs. The derivation of the evolutionary model requires the knowledge of the short-term ecological interactions between resident and mutant populations (with frozen values of the traits) and the statistics of the mutation process. All this is specified in the next two subsections (see [Ferrière *et al.*, 2002], for a more detailed description).

2.1. *Ecological dynamics*

The ecological interaction between species X (density x) and species Y (density y) is described by the following two ODEs:

$$\dot{x} = x(-r(u) - cx + vy(1 - \alpha x)), \tag{1a}$$

$$\dot{y} = y(-s(v) - dy + ux(1 - \beta y)). \tag{1b}$$

The mutualistic traits u and v are measured as per capita rates of commodities trading; thus, ux and vy represent the probabilities per unit time that one partner individual receives benefit from the mutualistic interaction. Intraspecific competition for commodities provided by the partner species is expressed by the linear density-dependent factors $(1-\alpha x)$ and $(1-\beta y)$ [Wolin, 1985]. The terms $-cx$ and $-dy$ measure the detrimental effect of intraspecific competition for other resources. The mutualism being obligate, the intrinsic rates of increase, $-r(u)$ and $-s(v)$, are negative, and $r(u)$ and $s(v)$ increase with u and v respectively, to reflect the direct cost of producing commodities. The functions $r(u) = r_1(u + u^2)$ and $s(v) = s_1(v + v^2)$ have been used to perform the numerical analysis, where

r_1 and s_1, as well as c, d, α, and β, are positive parameters.

The analysis of model (1) carried out in [Ferrière *et al.*, 2002] shows that the extinction equilibrium $(x, y) = (0, 0)$ is always locally stable (with respect to the positive orthant of the (x, y) plane) and that, depending on the trait values u and v, there may also exist two positive equilibria, one stable (a node, denoted by $(\overline{x}, \overline{y})$ in the following) and one unstable (saddle). The transition between the two cases (none or two positive equilibria) is a saddle-node bifurcation. Straightforward computations (see [Ferrière *et al.*, 2002, Appendix A]) give the condition satisfied by the model parameters at this bifurcation, as well as explicit formulas for $\overline{x}$ and $\overline{y}$. Specifically, if the stable equilibrium $(\overline{x}, \overline{y})$ exists, it is the larger real solution of

$$Ay^2 + By + C = 0, \tag{2}$$

where

$$\begin{aligned} A &= uv\beta + v\alpha d, \\ B &= -uv - ur(u)\beta + v\alpha s(v) + cd, \\ C &= ur(u) + cs(v), \end{aligned}$$

i.e. [see Eq. (1b)]

$$\overline{x}(u, v) = \frac{s(v) + d\overline{y}(u, v)}{u\,(1 - \beta\overline{y}(u, v))}, \tag{3a}$$

$$\overline{y}(u, v) = \frac{-B + \sqrt{B^2 - 4AC}}{2A}, \tag{3b}$$

and the bifurcation condition is the annihilation of the discriminant $B^2 - 4AC$ of Eq. (2). The corresponding bifurcation curve in the (u, v) trait space is the closed ovoid curve depicted in Fig. 1 (main panel), which defines the domain D of ecological viability of the mutualistic association. If (u, v) lies outside D, model (1) has no positive equilibria and the mutualistic association go extinct in the short-term, leaving no room for evolution (see Fig. 1, bottom-right panel). By contrast, if $(u, v) \in D$, then the two mutualistic partners can coexist at $(\overline{x}, \overline{y})$ (see Fig. 1, central panel), so that the mutation-selection processes can drive the evolution of the adaptive traits. Thus, the evolutionary dynamics of the traits u and v are only defined in the viable domain D.

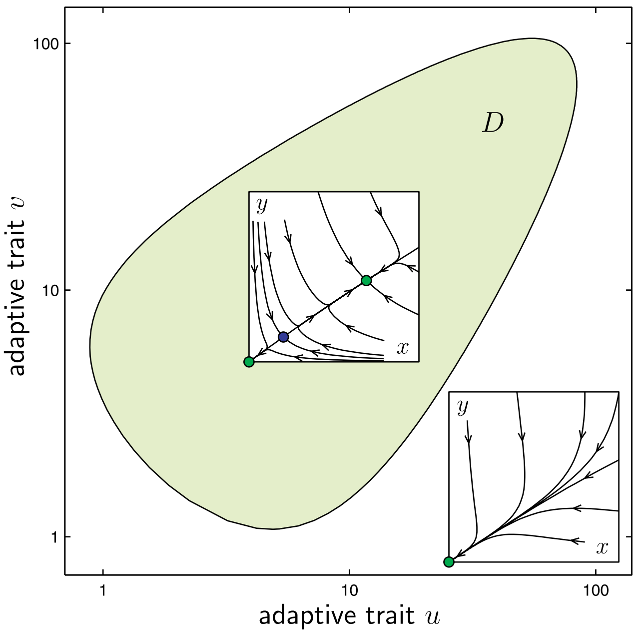

Fig. 1. The domain D of ecological viability of the mutualistic association in the trait space (u, v) (main panel) for the following parameter values: $c = 1$, $d = 2$, $\alpha = 2$, $\beta = 4$, $r_1 = s_1 = 10^{-3}$. For $(u, v) \notin D$ the two populations go extinct, as shown in the bottom-right state portrait (obtained for $u = v = 1$). For $(u, v) \in D$ steady coexistence of the two populations is possible, as shown in the central state portrait (obtained for $u = v = 1.8$). When the border of D is approached from inside, the stable equilibrium $(\overline{x}, \overline{y})$ (green circle) and the saddle (blue circle) become closer and closer until they collide (saddle-node bifurcation).

2.2. *Evolutionary dynamics*

To construct a mathematical model for the joint evolution of u and v, it is assumed that individuals' births, interactions, and deaths described by the ecological model (1) occur on a short, ecological, timescale over which the species abundances x and y quickly equilibrate at $(\overline{x}, \overline{y})$. Rare and small mutations in the traits arise on a long, evolutionary timescale. The evolutionary process comprises a sequence of trait substitutions caused by selection of successful mutants that win the competition against residents on the ecological timescale.

In order to derive the dynamics of the traits, one has to extend the ecological model (1) by considering the presence of a mutant population, i.e.

$$\begin{aligned} \dot{x} &= x(-r(u) - c(x + x_{\mathrm{mut}}) + vy(1 - a(0)x \\ &\qquad - a(u - u_{\mathrm{mut}})x_{\mathrm{mut}})), \qquad (4a) \\ \dot{x}_{\mathrm{mut}} &= x_{\mathrm{mut}}(-r(u_{\mathrm{mut}}) - c(x + x_{\mathrm{mut}}) \\ &\qquad + vy(1 - a(u_{\mathrm{mut}} - u)x - a(0)x_{\mathrm{mut}})), \qquad (4b) \\ \dot{y} &= y(-s(v) - dy + (ux + u_{\mathrm{mut}}x_{\mathrm{mut}}) \\ &\qquad \times (1 - b(0)y)), \qquad (4c) \end{aligned}$$

for the case of a mutant trait u_{mut} with population density x_{mut}, and

$$\begin{aligned}\dot{x} &= x(-r(u) - cx + (vy + v_{\text{mut}}y_{\text{mut}}) \\ &\quad \times (1 - a(0)x)), \qquad (5a)\\ \dot{y} &= y(-s(v) - d(y + y_{\text{mut}}) + ux(1 - b(0)y \\ &\quad - b(v - v_{\text{mut}})y_{\text{mut}})), \qquad (5b)\\ \dot{y}_{\text{mut}} &= y_{\text{mut}}(-s(v_{\text{mut}}) - d(y + y_{\text{mut}}) \\ &\quad + ux(1 - b(v_{\text{mut}} - v)y - b(0)y_{\text{mut}})), \qquad (5c)\end{aligned}$$

for the case of a mutant trait v_{mut} with population density y_{mut}. Equations (4) and (5) assume that intraspecific competition for commodities provided by the partner species is trait dependent and described by the functions a and b. In particular, $a(0) = \alpha$ and $b(0) = \beta$, so that Eqs. (4) and (5) degenerate into the ecological model (1) if the mutant is absent. Denoting by $-\alpha'$ and $-\beta'$ the slopes of a and b when $u_{\text{mut}} = u$ and $v_{\text{mut}} = v$ respectively, parameters α' and β' measure the degrees of competitive asymmetry for commodities provided by the partner in species X and Y. Positive values of α' [β'] reflect a competitive advantage for slightly better mutualistic mutants in species X [Y], i.e. a premium for providing more commodities; conversely, negative values of α' [β'] reflect a competitive advantage for slightly less mutualistic mutants (cheaters); if $\alpha' = 0$ [$\beta' = 0$] competition is symmetric.

By assuming the timescale separation of ecological and evolutionary processes, and in the limit of infinitesimally small mutations, the approach of adaptive dynamics theory [Dieckmann & Law, 1996; Metz *et al.*, 1996; Geritz *et al.*, 1997, 1998] provides a deterministic approximation of the underlaying stochastic processes of mutation and selection. The final result is that the traits u and v vary in accordance with the following two ODEs:

$$\dot{u} = k_u\overline{x}(u, v)\, \frac{\partial W_X}{\partial u_{\text{mut}}}\, (u_{\text{mut}}, u, v)\bigg|_{u_{\text{mut}}=u}, \qquad (6a)$$

$$\dot{v} = k_v\overline{y}(u, v)\, \frac{\partial W_Y}{\partial v_{\text{mut}}}\, (v_{\text{mut}}, u, v)\bigg|_{v_{\text{mut}}=v}, \qquad (6b)$$

where $\overline{x}(u, v)$ and $\overline{y}(u, v)$ are given by Eq. (3), parameters k_u and k_v are proportional to the frequency and variance of small mutations in species X and Y, and W_X and W_Y are the so-called invasion fitnesses, defined as per capita rates of increase from initial scarcity of the mutant populations x_{mut} and y_{mut} in a resident association (u, v) settled at $(\overline{x}, \overline{y})$ [Metz *et al.*, 1992].

In formulas:

$$\begin{aligned}W_X(u_{\text{mut}}, u, v) &= \frac{\dot{x}_{\text{mut}}}{x_{\text{mut}}}\bigg|_{\substack{x_{\text{mut}}=0\\ x=\overline{x}(u,v)\\ y=\overline{y}(u,v)}} \\ &= -r(u_{\text{mut}}) - c\overline{x}(u, v) + v\overline{y}(u, v) \\ &\quad \times (1 - a(u_{\text{mut}} - u)\overline{x}(u, v)),\\ W_Y(v_{\text{mut}}, u, v) &= \frac{\dot{y}_{\text{mut}}}{y_{\text{mut}}}\bigg|_{\substack{y_{\text{mut}}=0\\ x=\overline{x}(u,v)\\ y=\overline{y}(u,v)}} \\ &= -s(v_{\text{mut}}) - d\overline{y}(u, v) + u\overline{x}(u, v) \\ &\quad \times (1 - b(v_{\text{mut}} - v)\overline{y}(u, v)),\end{aligned}$$

so that the evolutionary model (6) becomes:

$$\dot{u} = k_u\overline{x}(u, v)\left(-\frac{dr}{du}(u) + \alpha' v\overline{x}(u, v)\overline{y}(u, v)\right), \qquad (7a)$$

$$\dot{v} = k_v\overline{y}(u, v)\left(-\frac{ds}{dv}(v) + \beta' u\overline{x}(u, v)\overline{y}(u, v)\right), \qquad (7b)$$

for (u, v) in the domain D (see Sec. 2.1). Along an evolutionary orbit $(u(t), v(t))$ of model (7) the population densities x and y track the equilibrium densities (3) corresponding to the current trait values, i.e. $(\overline{x}(u(t), v(t)), \overline{y}(u(t), v(t)))$. If the evolutionary orbit reaches the border of D both coevolving populations undergo an evolutionary suicide.

3. Bifurcation Analysis of the Evolutionary Model

Now the unfolding of standard and border collision bifurcations of the evolutionary model (7) is presented with respect to the degrees of competitive asymmetry for commodities α' and β'. (The other parameters are kept constant at the values reported in the caption of Fig. 1.)

In biological terms, the existence of an attractor of model (7) for positive values of α' and β' is consistent with the conjecture that a competitive premium for good mutualists is the key for the long-term persistence of interspecific mutualism. In fact, for nonpositive α' and β', the rates of change $\dot{u}$ and $\dot{v}$ of the traits u and v given by Eqs. (7) are negative for all (u, v) in the domain D of ecological viability, and evolutionary suicide is the inevitable outcome (see Fig. 2).

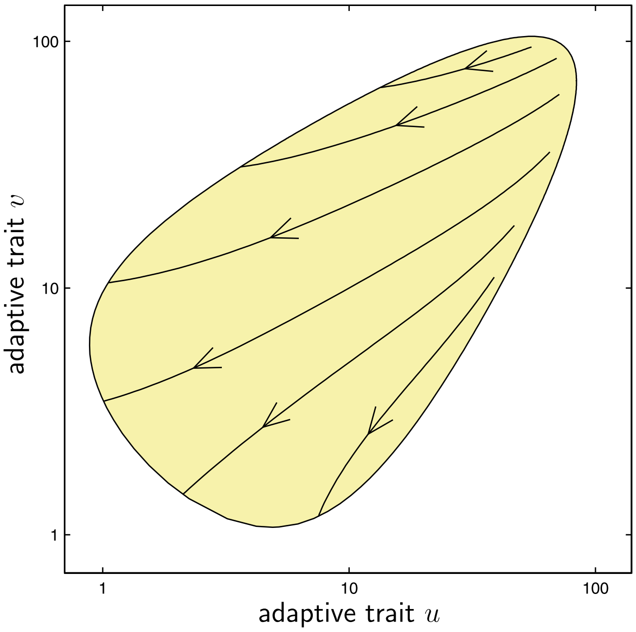

Fig. 2. Evolutionary dynamics in the plane of the adaptive traits (u, v) under symmetric competition for commodities provided by the partner species ($\alpha' = \beta' = 0$, other parameter values as in Fig. 1). Yellow area: set of ancestral conditions leading to evolutionary suicide. Coevolution is characterized by mutualism disinvestment ($\dot{u} < 0$, $\dot{v} < 0$ for all (u, v) in the domain D of ecological viability). Evolutionary suicide is the final outcome irrespective to ancestral conditions.

Figure 3 shows the bifurcation diagram and unravels seven qualitatively different evolutionary state portraits depicted in Fig. 4. Notice that the border of the domain D of ecological viability is independent of α' and β', and that the state portraits corresponding to regions ④′–⑥′ are not shown (they are almost symmetric copies of those corresponding to regions ④–⑥ with respect to the diagonal $u = v$; the symmetry, however, is not exact since $\alpha \neq \beta$ and $c \neq d$, see caption of Fig. 1). Curves and points in Fig. 3 correspond to codimension-1 and -2 standard or border collision bifurcations. The type of bifurcation is indicated in the caption (see e.g. [Kuznetsov, 1998] for standard codimension-1 and -2 bifurcations). The two thin gray areas in the main panel hide more complex bifurcation structures than a single bifurcation curve. Such structures are not visible at the scale of the main panel and are unraveled by four magnified views in suitable neighborhoods of the codimension-2 bifurcation points BT_1, A_1, A_2, BT_2 (right panels).

Figures 3 and 4 are self-explaining and show that asymmetric competition for commodities provided by the partner species, with a competitive premium for good mutualists, can indeed explain the evolutionary persistence of interspecific mutualism. The region of the (α', β') plane in which this is possible is the union of regions ①, ⑤–⑦, ⑤′, ⑥′, the long-term evolutionary regime being stationary in regions ①, ⑤, and ⑤′, cyclic in region ⑦, and stationary or cyclic in regions ⑥ and ⑥′. However, evolutionary suicide is always possible for suitable ancestral conditions (see yellow areas in Fig. 4), and this may turn the empirical test of theoretical results problematic.

All bifurcation curves shown in Fig. 3 have been numerically produced by standard continuation techniques [Doedel *et al.*, 1991a, 1991b] using the software package AUTO97 [Doedel *et al.*, 1997].

Producing a bifurcation curve requires two steps. First the bifurcation needs to be detected, by continuing an invariant with respect to one parameter. The detection is performed by monitoring a suitable *test function* which is null when the invariant undergoes the bifurcation. Then, the bifurcation curve needs to be traced in a parameter plane, by continuing (with respect to two parameters) a set of equations, called *defining system* of the bifurcation, which identifies the bifurcation. Test functions and defining systems are implemented in AUTO97 for standard bifurcations, but not for border collision bifurcations.

Two types of border collision bifurcations are present in Fig. 3, namely the collision of an equilibrium or that of a limit cycle of model (7) with the border of the domain D. Using the terminology introduced for Filippov systems (see e.g. [Bernardo di *et al.*, 2001; Kuznetsov *et al.*, 2003]), such bifurcations are here called *boundary equilibrium* and *grazing* respectively.

A boundary equilibrium bifurcation can be detected by finding a zero of the discriminant $\Delta = B^2 - 4AC$ of Eq. (2), since $\Delta = 0$ when (u, v) reaches the border of D. However, model (7) is not defined for $\Delta < 0$ (see Eq. (3b)), so that a zero of Δ can hardly be detected, in practice. In fact, numerical continuation proceeds in a prediction-correction fashion, where predictions are made along the tangent direction to the solution branch, according to a (possibly adaptive) stepsize, and corrections are based on Newton's method [Doedel *et al.*, 1991a, 1991b]. Thus, in order to find the zero of a test function, a change of sign of such a function from one step to the next needs first to be detected; then, subsequent refinements locate the zero within the desired accuracy. A boundary

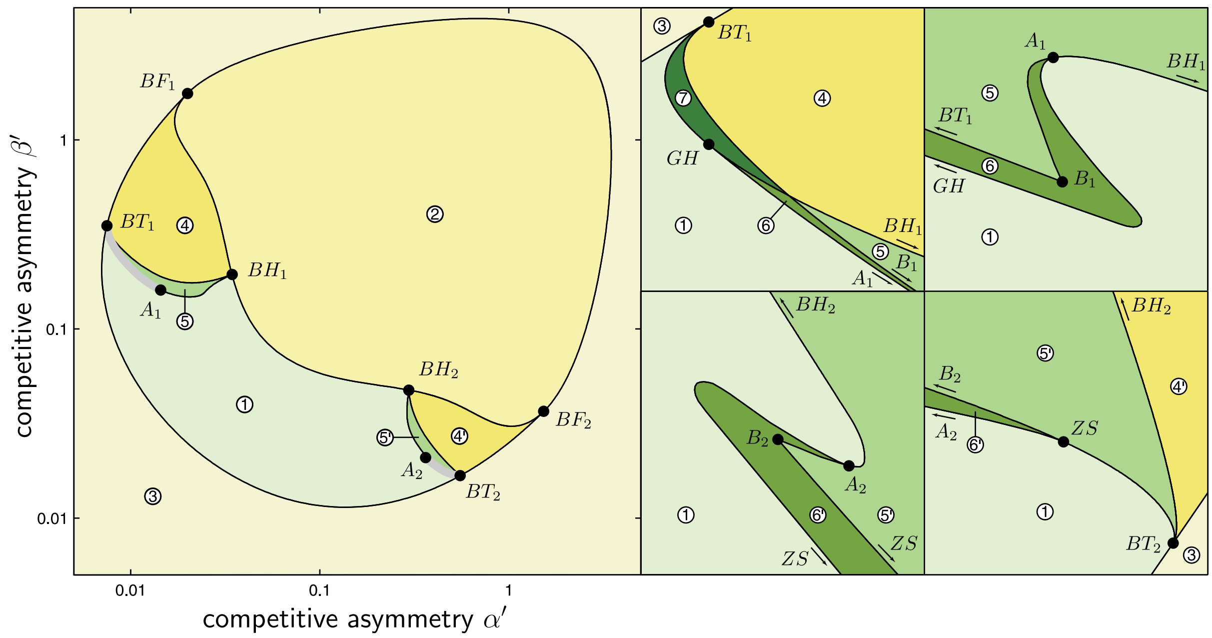

Fig. 3. Bifurcation diagram of the evolutionary model (7) in the (α', β') plane: Main panel (left) plus four magnified views in suitable neighborhoods of points BT_1, A_1, A_2, BT_2 (right panels, arrows indicate terminal points of bifurcation curves lying outside the panel), illustrating the bifurcation structures covered by the two thin gray areas in the main panel. Other parameter values are as in Fig. 1. Bifurcation curves: A_1–B_1, A_2–B_2, grazing (of stable cycle); A_1–BH_1, A_2–BH_2, grazing (of unstable cycle); A_1–GH, A_2–ZS, tangent of cycles (stretched for purpose of illustration); B_1–BT_1, B_2–ZS, homoclinic (negative saddle quantity); BF_1–BF_2, boundary saddle; BF_1–$BH_{1,2}$–BF_2, boundary node/focus; BF_1–$BT_{1,2}$–BF_2, saddle-node; BH_1–GH, BH_2–BT_2, subcritical Hopf; BT_1–GH, supercritical Hopf; BT_2–ZS, homoclinic (positive saddle quantity). Codimension-2 bifurcation points: A_1, A_2, tangent of grazing cycles; B_1, B_2, grazing homoclinic; BF_1, BF_2, boundary saddle-node; BH_1, BH_2, boundary Hopf; BT_1, BT_2, Bogdanov–Takens; GH, generalized Hopf; ZS, zero saddle quantity.

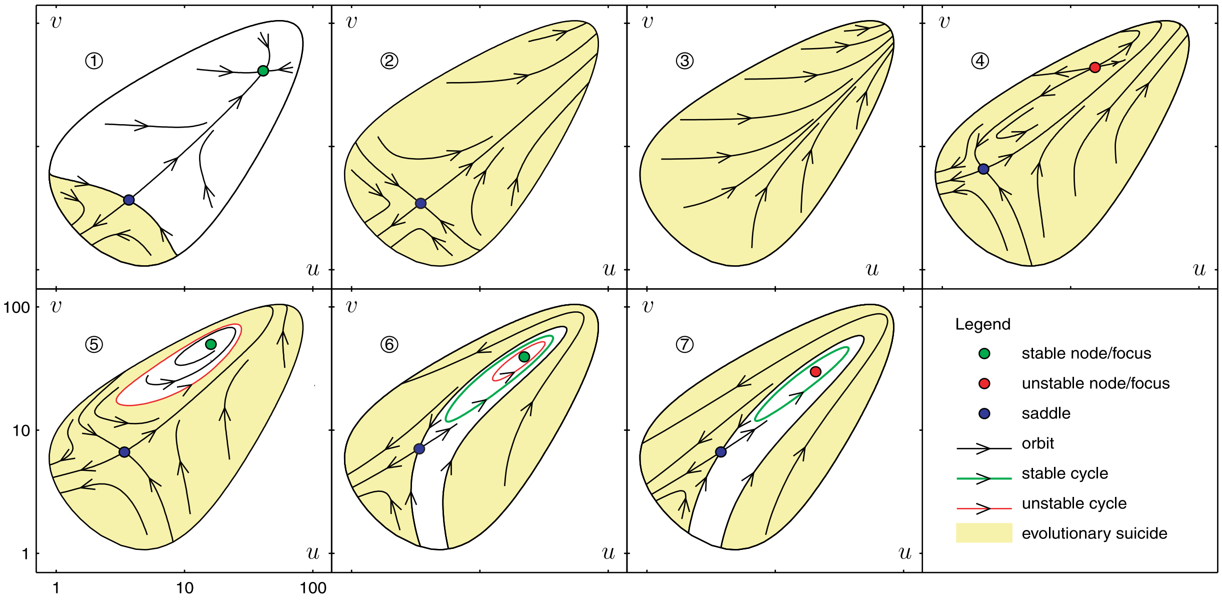

Fig. 4. Evolutionary dynamics in the plane of the adaptive traits (u, v) for different degrees of competitive asymmetry for commodities (same scale in all panels). Yellow areas: set of ancestral conditions leading to evolutionary suicide. Numbering refers to the corresponding regions of Fig. 3: ① $\alpha' = 0.04$, $\beta' = 0.04$; ② $\alpha' = 0.4$, $\beta' = 0.4$; ③ $\alpha' = 4$, $\beta' = 4$; ④ $\alpha' = 0.015$, $\beta' = 0.4$; ⑤ $\alpha' = 0.015$, $\beta' = 0.17$; ⑥ $\alpha' = 0.007484$, $\beta' = 0.3406$; ⑦ $\alpha' = 0.007464$, $\beta' = 0.3470$. Some evolutionary orbits are stretched for purpose of illustration. Other parameter values are as in Fig. 1.

equilibrium bifurcation of model (7) can therefore be detected approximately by substituting the test function Δ with $\Delta - \delta$, with a small $\delta > 0$ and using a sufficiently small continuation step-size.

As for the continuation of a boundary equilibrium bifurcation, if model (7) is written in the form

$$\begin{aligned}\dot{u} &= f_u(u, v, \alpha', \beta'),\\ \dot{v} &= f_v(u, v, \alpha', \beta'),\end{aligned}$$

then the defining system is:

$$f_u(u, v, \alpha', \beta') = 0, \tag{8a}$$

$$f_v(u, v, \alpha', \beta') = 0, \tag{8b}$$

$$\Delta(u, v, \alpha', \beta') = 0. \tag{8c}$$

Equations (8a) and (8b) say that (u, v) is an equilibrium of model (7), while Eq. (8c) requires that (u, v) lies on the border of D. Unfortunately, the continuation of Eq. (8) with respect to (α', β') inevitably crashes as soon as a prediction of the continuation algorithm involves a slightly negative value of Δ. But when $\Delta = 0$, the ecological equilibrium $(\overline{x}, \overline{y})$ is simply given by (see Eqs. (3))

$$\hat{x}(u, v) = \frac{s(v) + d\hat{y}(u, v)}{u(1 - \beta\hat{y}(u, v))}, \quad \hat{y}(u, v) = -\frac{B}{2A},$$

so that the defining system becomes:

$$-\frac{dr}{du}(u) + \alpha' v\hat{x}(u, v)\hat{y}(u, v) = 0, \tag{9a}$$

$$-\frac{ds}{dv}(v) + \beta' u\hat{x}(u, v)\hat{y}(u, v) = 0, \tag{9b}$$

$$\Delta(u, v, \alpha', \beta') = 0, \tag{9c}$$

which is well defined even for $\Delta < 0$. The algebraic system (9) is composed of three scalar equations and defined in the four-dimensional space (u, v, α', β'). Thus, it generically admits one-dimensional solution branches which, projected in the (α', β') plane, give boundary equilibrium bifurcation curves.

The analysis of grazing bifurcations is slightly more complex. If $(u(t; \alpha', \beta'), v(t; \alpha', \beta'))$, $t \in [0, T(\alpha', \beta')]$, is a T-periodic parametric solution family of model (7), then

$$\min_{t\in[0,T(\alpha',\beta')]} \{\Delta(u(t; \alpha', \beta'), v(t; \alpha', \beta'), \alpha', \beta')\} \tag{10}$$

is a test function that can be used for detecting a grazing bifurcation, during the continuation of a limit cycle of model (7). However, since model (7) is not defined for $\Delta < 0$, a zero of function (10) cannot be detected, in practice. As in the case of boundary equilibrium bifurcations, a grazing bifurcation of model (7) could be approximately detected by finding a zero of the following function:

$$\min_{t\in[0,T(\alpha',\beta')]} \{\Delta(u(t; \alpha', \beta'), v(t; \alpha', \beta'), \alpha', \beta')\} - \delta,$$

with a small $\delta > 0$. However, only a finite number N of points, (u_k, v_k), $k = 1, \ldots, N$, of a limit cycle are continued, i.e. those corresponding to a finite mesh, $0 = t_0 < t_1 < \cdots < t_N = T$, defined on the time interval $[0, T]$ [Doedel *et al.*, 1991b]. A suitable test function is therefore:

$$\min_{k=1,\ldots,N} \{\Delta(u_k, v_k, \alpha', \beta')\} - \delta.$$

As for the continuation of a grazing bifurcation, the defining system is:

$$\dot{p} - Tf_u(p, q, \alpha', \beta') = 0, \tag{11a}$$

$$\dot{q} - Tf_v(p, q, \alpha', \beta') = 0, \tag{11b}$$

$$p(0) - p(1) = 0, \tag{11c}$$

$$q(0) - q(1) = 0, \tag{11d}$$

$$\Delta(p(0), q(0), \alpha', \beta') = 0, \tag{11e}$$

$$\begin{aligned}&\frac{\partial\Delta}{\partial u}(p(0), q(0), \alpha', \beta')f_u(p(0), q(0), \alpha', \beta')\\ &\quad + \frac{\partial\Delta}{\partial v}(p(0), q(0), \alpha', \beta')f_v(p(0), q(0), \alpha', \beta') = 0.\end{aligned} \tag{11f}$$

Equations (11a) and (11b) are a time-scaled version of model (7) (T is the period of the solution $(u(t) = p(t/T), v(t) = q(t/T))$). Periodicity is ensured by Eqs. (11c) and (11d), while Eqs. (11e) and (11f) require that the solution starts tangentially to the border of D at time $t = 0$. Unfortunately, analogously to Eq. (8), Eq. (11) cannot be used, in practice, and the grazing bifurcations of model (7) can only by approximated by substituting Eq. (11e) with

$$\Delta(p(0), q(0), \alpha', \beta') - \delta = 0 \tag{12}$$

with a small $\delta > 0$. Equations (12) and (11f) say that the solution starts, at time $t = 0$, tangentially to the curve defined by $\Delta = \delta$, which bounds a domain contained in D and as close to D as δ is small. The defining system [(11a)–(11d), (11f), (12)] is a boundary-value continuation problem in the $[0, 1]$ time interval, composed of 2 ODEs and four scalar boundary conditions, and defined in the seven-dimensional space $(p(0), q(0), p(1), q(1), T, \alpha', \beta')$. Thus, it generically admits one-dimensional solution branches which, projected in the (α', β') plane, give approximated grazing bifurcation curves (see Appendix for the validity of such an approximation in Fig. 3).

The defining systems (9) and [(11a)–(11d), (11f), (12)] can be easily implemented in AUTO97. However, generic n-dimensional versions have been recently implemented in SLIDECONT [Dercole & Kuznetsov, 2005], a software package for numerical bifurcation analysis of Filippov systems.

4. Discussion and Conclusions

The theoretical analysis presented in [Ferrière *et al.*, 2002] and complemented in this paper shows that asymmetrical intraspecific competition for the commodities offered by mutualistic partners provides a simple and testable ecological mechanism that can account for the long-term persistence of mutualisms. Cheating, in effect, establishes a background against which better mutualists can display any competitive superiority. This can lead to the evolutionary coexistence of mutualist and cheater traits, even though natural selection can drive certain ancestral evolutionary states to the evolutionary suicide of the mutualistic partners. These results are in agreement with empirical findings indicating that associations of mutualists and cheaters have existed over long spans of evolutionary time [Machado *et al.*, 1996; Pellmyr *et al.*, 1996; Pellmyr & Leebens-Mack, 1999; Després & Jaeger, 1999; Bronstein, 2001], and that intraspecific competition for commodities is indeed asymmetrical and in favor of good mutualists [Addicott, 1985; Bull & Rice, 1991; Christensen *et al.*, 1991; Mitchell, 1994; Iwasa *et al.*, 1995; Anstett *et al.*, 1998; Bultman *et al.*, 2000].

The mathematical description consists of two models: the ecological model (1), accounting for the short-term dynamics of the abundances of two mutualistic populations for frozen values of the adaptive traits (rates of commodity provision), and the evolutionary model (7), governing the long-term dynamics of the traits.

The analysis of the ecological model shows that steady coexistence of the mutualistic pair is possible as long as the traits are neither extremely low nor too high. At the boundary of the domain D of trait space where ecological persistence is possible (i.e. on the ovoid curve in Fig. 1), the system undergoes a catastrophic bifurcation (saddle-node) and collapses abruptly. In the short-term, within the persistence region, mutualistic populations reach a stable ecological equilibrium. However, ecological coexistence alone by no means provides a sufficient condition for the long-term persistence of a mutualism: an evolutionary perspective is mandatory.

The analysis of the evolutionary model shows that if individuals compete with equal success for the commodity provided by the other species, regardless of how much those individuals invest in mutualism (symmetrical competition), or if asymmetrical competition favoring good mutualists is too weak (bottom-left part of region ③ in Fig. 3) the mutualism erodes because cheating mutants that invest less in mutualism will be under no competitive disadvantage and thus will always be able to invade, ultimately driving the partner species toward the bottom-left part of the boundary of the coexistence region D, irrespectively to the ancestral state (see Fig. 2). If the asymmetry is very strong at least in one species (top or right part of region ③ in Fig. 3), the selective pressure favoring the provision of more commodities will predominate, causing runaway selection until the costs incurred are so large that the mutualistic association becomes nonviable and extinction is again the inexorable outcome (see Fig. 4 panel ③). By contrast, at intermediate degrees of competitive asymmetry, the association can evolve toward viable stationary or cyclic long-term evolutionary regimes (see regions ①, ⑤–⑦, ⑤′, ⑥′ in Fig. 3 and corresponding panels in Fig. 4).

Since evolutionary dynamics are confined in the domain of ecological viability, both standard and border collision bifurcations will generically occur. Notice that a border collision bifurcation involving an evolutionary attractor implies an abrupt rise of the risk of evolutionary extinction. In fact, through such a bifurcation, the basin of attraction of the bifurcating attractor becomes part of the set of ancestral conditions leading to evolutionary suicide (see the boundary equilibrium bifurcation from region ① to region ② and the grazing bifurcation from region ⑥ to region ⑤ in Fig. 3, and corresponding evolutionary state portraits in Fig. 4, where the yellow area rises abruptly through the bifurcations).

This paper has shown how boundary equilibrium and grazing bifurcations can be detected and continued in parameter space, in generic

n-dimensional vector fields. The biological message of this study is that the systematic detection and continuation of border collision bifurcations in parameter space is of crucial importance for the full understanding of the links between ecology and evolution. Though linking ecology and evolution is perhaps one of the challenges of the 21st century in biology, I believe that the value of the numerical techniques presented in this paper is even wider. In fact, border collision bifurcations are common to several classes of dynamical systems, which have been used in a variety of applications in very different areas of engineering and applied sciences.

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Appendix

Two indicators of the degree of approximation of a grazing bifurcation curve of model (7) computed by means of Eqs. [(11a)–(11d), (11f), (12)] are

$$\max_i \left\{ \frac{\min_{s\in\mathbf{R}}\{\|(u(0;\alpha_i',\beta_i') - u_D(s;\alpha_i',\beta_i'), v(0;\alpha_i',\beta_i') - v_D(s;\alpha_i',\beta_i'))\|\}}{\|(u(0;\alpha_i',\beta_i'), v(0;\alpha_i',\beta_i'))\|} \right\} \tag{A.1}$$

and

$$\max_i \left\{ \frac{\min_{s\in\mathbf{R}}\left\{\|(\alpha_i' - \alpha'(s), \beta_i' - \beta'(s))\|\right\}}{\|(\alpha_i',\beta_i')\|} \right\}, \tag{A.2}$$

where (α_i', β_i') is the ith point of the computed solution branch (say for $\delta = \overline{\delta}$), $(u_D(s;\ \alpha_i',\ \beta_i'),$ $v_D(s;\ \alpha_i',\ \beta_i'))$ is a parametrization of the border of D, $(\alpha'(s), \beta'(s))$ is a parametrization of the (not known) grazing bifurcation curve, and $\|\cdot\|$ is the Euclidean norm in $\mathbf{R}^2$.

Indicators (A.1) and (A.2) respectively measure the maximum (relative) distance, along the solution branch, in trait space between the continued cycle and the border of D, and in parameter space between the approximated and the real grazing bifurcation curves. When small, they are well approximated by

$$\max_i \left\{ \frac{\delta \Big/ \left\| \left(\frac{\partial \Delta}{\partial u}(u(0;\alpha_i',\beta_i'), v(0;\alpha_i',\beta_i'), \alpha_i', \beta_i'), \frac{\partial \Delta}{\partial v}(u(0;\alpha_i',\beta_i'), v(0;\alpha_i',\beta_i'), \alpha_i', \beta_i') \right) \right\|}{\|(u(0;\alpha_i',\beta_i'), v(0;\alpha_i',\beta_i'))\|} \right\} \tag{A.3}$$

and

$$\max_i \left\{ \frac{\frac{\delta}{\epsilon} \min_j \{\|(\alpha_i' - \alpha_j', \beta_i' - \beta_j')\|\}}{\|(\alpha_i',\beta_i')\|} \right\}, \tag{A.4}$$

where (α_j', β_j') is the jth point of a solution branch of Eqs. [(11a)–(11d), (11f), (12)] computed for $\delta = \overline{\delta} + \epsilon$.

The grazing bifurcation curves shown in Fig. 3 have been computed for $\overline{\delta} = 1$ and $\epsilon = 1$, and the obtained indicators (A.3) and (A.4) are smaller than 10^{-5}.