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Interim Report **IR-06-006**

Coevolution of Slow-fast Populations: Evolutionary Sliding, Evolutionary Pseudo-equilibria, and Complex Red Queen Dynamics

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Contents

COEVOLUTION OF SLOW-FAST POPULATIONS: EVOLUTIONARY SLIDING, EVOLUTIONARY PSEUDO-EQUILIBRIA, AND COMPLEX RED QUEEN DYNAMICS

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Running title: Coevolution of slow-fast populations

Abstract

We study the interplay of ecological and evolutionary dynamics in communities composed of populations with contrasting timescales. In such communities, genetic variations of individual traits can cause population transitions between stationary and cyclic ecological regimes, hence abrupt variations in fitness. Such abrupt variations raise ridges in the adaptive landscape where the populations are poised between equilibrium and cyclic coexistence and along which evolutionary trajectories can remain sliding for long times or halt at special points called evolutionary pseudo-equilibria. These novel phenomena should be generic to all systems in which ecological interactions cause fitness to vary discontinuously. They are demonstrated by the analysis of a predator-prey community, with one adaptive trait for each population. The eco-evolutionary dynamics of the system show a number of other distinctive features, including evolutionary extinction and two forms of Red Queen dynamics. One of them is characterised by intermittent bouts of cyclic oscillations of the two populations.

Key words: slow-fast population dynamics, eco-evolutionary dynamics, Red Queen dynamics, evolutionary sliding and pseudo-equilibria, adaptive ridge, predator-prey coevolution.

1 Introduction

Understanding the determinants of population dynamics is an important theme throughout biology, from human health to conservation. In studying population dynamics, much research has addressed how ecological interactions affect population stability yet ignoring the genetic diversity and ensuing evolvability of populations. Ford (1949) was perhaps the first to document that evolutionary change and population dynamics can occur interdependently; Pimentel (1968), Stenseth and Maynard Smith (1984) and Metz et al. (1992) subsequently conceptualised the notion of the ecological and evolutionary dynamics of a population being entangled in a feedback loop. The dynamical interplay of ecology and evolution prompts three general questions (May and Anderson, 1983; Ferrière and Gatto, 1993, 1995; Abrams, 2000): (1) How does evolution of adaptive traits affect the ecological stability of a community? (2) Under which conditions are ecological interactions expected to beget fluctuations in a population's genetic state? (3) How do eco-evolutionary dynamics respond to environmental change?

Although a significant number of studies have dealt with some aspects of these three questions, there has been so far no attempt to address them simultaneously in a unified framework. Moreover, most models of the adaptive evolution of traits related to inter- and/or intra-specific interactions have assumed stable ecological equilibria for all trait values in the relevant trait space. This study aims at developing a unified analysis of eco-evolutionary dynamics in communities containing "slow" and "fast" populations, which allows us to relax the ecological equilibrium assumption.

Slow-fast systems are composed of populations whose ecological fluctuations develop on contrasting timescales. Predator-prey communities offer many instances of contrasting ecological timescales. Prey are often smaller than predator, hence faster in growing and reproducing. In the plankton food chain, the turnover of algae is faster than that of most zooplankton species which, in turn, grow faster than fish (Scheffer, 1998). The Boreal forest is also rich of examples: plants (forbs and grasses) have fast dynamics in comparison with most herbivores (hares, squirrel, and small rodents) which reproduce faster than their predators (lynx, coyote, and red fox) (Stenseth et al., 1997). The opposite case, namely that of slow prey and fast predator, is also frequently observed in nature—spruce budworm (Ludwig et al., 1978) and larch budmoth (Baltensweiler, 1971) provide typical examples among plant-insect interactions. Hereafter we investigate theoretically the coevolution of a slow predator and fast prey. This analysis will serve to demonstrate the general features of eco-evolutionary dynamics of slow-fast populations that we first outline qualitatively in the following section.

2 Coevolutionary dynamics of slow-fast populations: general results

Eco-evolutionary processes generally assume two main ingredients: genetically-based variations of individual traits generated through reproduction, and selection on this variation resulting from ecological interactions. This is a complex process because individual traits under consideration may affect both the birth process and the ecological interactions. The assumption of rare mutations of small effects allows one to approximate the dynamics of population densities and trait distributions with deterministic models.

In the limit of rare mutations of small effects, the rate of change of an adaptive trait over evolutionary time is proportional to the resident population birth output per unit time (proportional to the probability that a mutation occurs within a small time interval), and to the derivative, with respect to mutant's trait, of the per-capita rate of increase of a mutant population per generation (when positive, proportional to the probability of mutant non-extinction) (Metz et al., 1996). In the general situation of a trait z, resident population density n at equilibrium, per-capita birth rate β (i.e. $1/\beta$ is the expected time between birth), mutant's trait z' and instantaneous per-capita rate of increase S, this translates into the so-called canonical equation of adaptive dynamics (Dieckmann and Law, 1996):

$$\dot{z} = k\,(\beta n)\left(\frac{s}{\beta}\right) \tag{1}$$

where $s = \partial S/\partial z'|_{z'=z}$ is called selection derivative, and k is a parameter proportional to the probability that an offspring is a mutant and to the variance of mutation. Since the resident population density is at equilibrium, this equation simplifies as both β cancel out.

Here we need an extension of eq. (1) to the case of more general resident population attractors. The rigorous derivation of such an extension is a hard mathematical exercise that lies beyond the scope of this paper (see Dieckmann and Law, 1996, for a heuristic discussion of the problem). However, as explained below, averaging the mutation term, (βn), and selection term, (s/β), over the attractor is appropriate in the case considered in this paper. In formulas, this results in

$$\dot{z} = k\,\langle \beta n\rangle \left\langle \frac{s}{\beta}\right\rangle \tag{2}$$

where brackets indicate temporal averaging over the resident population attractor.

At this point, the analysis of eco-evolutionary dynamics through eq. (2) would remain problematic because, in general, the resident population attractor is not known analytically in closed form. Slow-fast systems represent a significant exception to this predicament. Indeed, any slow-fast population attractor can be approximated with the so-called *singular attractor* corresponding to completely separated timescales (Rinaldi and Scheffer, 2000), and this permits explicit calculation of the averages in eq. (2). The case of slow-predator-fast-prey limit cycles is particularly favourable because the cycle can be easily identified. Moreover, such cycles are characterised by long phases of slow motion of both populations alternating with fast phases of significant prey variation. Thus, slow-fast cycles are very long, so that mutant populations experience little variations in the resident state during their initial phase of growth or decline (with the only exception of particular mutations occurring during the short episodes of fast variation of the prey). This supports the use of eq. (2) which indeed takes the expectation of (βn) and (s/β) over all possible resident states at the time of mutant arising.

A key evolutionary consequence of slow-fast ecological interactions is that the selection pressure becomes discontinuous across the trait space when stationary and cyclic coexistence are possible for different combinations of the traits. This is so because the transition from an equilibrium to a singular cycle is discontinuous (Rinaldi and Scheffer, 2000). General implications for eco-evolutionary dynamics can be outlined by focusing on two populations, e.g. a prey and a predator, coevolving in a two-dimensional trait space. Predator-prey interactions have long been known for their potential to generate a whole spectrum of ecological dynamics in response to variation in individual trait values, from extinction to stable equilibria and cycles. Thus, the trait space splits in three regions: extinction of at least one population in $\mathcal{E}$, stationary coexistence in $\mathcal{S}$, and cyclic coexistence in $\mathcal{C}$. The selection pressure driving the dynamics of the two traits is continuous inside region $\mathcal{S}$ and region $\mathcal{C}$ but it is discontinuous at the boundary separating $\mathcal{S}$ and $\mathcal{C}$. Two different evolutionary gradients are associated to each point of the boundary: one is the vector tangent to the evolutionary trajectory driven by the selection pressure operating in region $\mathcal{S}$ and the other is the vector tangent to the evolutionary trajectory driven by the selection pressure operating in region $\mathcal{C}$ (see Fig. 1 for an example). If the transversal components of these two vectors with respect to the discontinuity boundary have the same sign, as in Fig. 1A (dotted part of the discontinuity boundary), the trajectory crosses the boundary and the populations switch from cyclic to stationary (or viceversa). On the contrary, if the transversal components of the two vectors are of opposite sign, i.e. if the two evolutionary gradients are "pushing" in opposite directions, (solid part of the discontinuity boundary in Fig. 1), the traits are forced to remain on the boundary and "slide" on it. In other words, the boundary separating the two possible ecological regimes can raise an attractive *ridge* in the adaptive landscape, along which evolutionary trajectories from various ancestral conditions are canalised. The evolution on the ridge can be temporary, as in Fig. 1A where the sliding motion terminates at point T, or permanent, when the sliding motion halts at a so-called *pseudo-equilibrium*, namely at a point P on the boundary (see Fig. 1B) where the two evolutionary gradients align. A pseudo-equilibrium has all the properties of an equilibrium (in particular it can be an attractor, a saddle or a repellor) even if the selection pressures do not vanish at that point.

The rest of the paper focuses on a specific predator-prey model to demonstrate patterns of evolutionary sliding and pseudo-equilibria, and to recast them among other distinctive features of predator-prey coevolution. Such features include enhancement of Red Queen dynamics through the increase of genetic variation of the prey, generic occurrence of evolutionary extinction in the predator, and coevolution acting against ecological destabilisation resulting from environmental enrichment.

3 A model of predator-prey eco-evolutionary dynamics

Our presentation of a specific model of slow-fast populations and their eco-evolutionary dynamics focuses on the main features of the model, while details on mathematical derivations and approximations are relegated into the (electronic) Appendix.

The predator-prey model we consider is the so-called Rosenzweig-MacArthur model (Rosenzweig and MacArthur, 1963) composed of a logistic prey and a Holling-type II predator:

$$\dot{x}(t) = x(t)\left[r\left(1-\frac{x(t)}{K}\right)-\frac{a\,y(t)}{h+x(t)}\right] \tag{3}$$

$$\dot{y}(t) = y(t)\left[b+e\frac{a\,x(t)}{h+x(t)}-d\right] \tag{4}$$

where $x(t)$ and $y(t)$ are prey and predator population densities at time t. In the absence of predator the prey population grows logistically (with intrinsic growth rate r and carrying capacity K), while in the absence of prey the predator population decays exponentially (the intrinsic birth rate b is smaller than the death rate d but the maximum birth rate $(b+ea)$ is greater than d). The maximum predation rate is a, the functional response half-saturation constant is h, and the extra natality resulting from predation is proportional to the predation rate through an efficiency coefficient e. The presence of a saturating functional response makes stationary and cyclic coexistence possible for different parameter settings (Section A1 in Appendix). The limit cycle is not known analytically, yet if prey grow at a much faster rate than predators, it can be approximated by the singular limit cycle (derived algebraically in Section A2 in Appendix).

Let u and v denote the adaptive traits for the prey and predator, respectively. Assume that the prey has density- and trait-independent birth rate, while its death rate has a density-dependent component controlled by u. Thus, in eq. (3) r is constant while K depends on u. We further assume that K peaks at u_0, for which the prey is most effective. Similarly, the predator intrinsic birth rate b is constant, while its death rate d depends upon v and is minimum at v_0, at which predators are best adapted to their environment. The predation rate is a function of both traits, and predator [prey] benefit [lose] most from the interaction when traits are balanced, i.e. when u and v are in a suitable relationship, which defines a "bidirectional axis of prey vulnerability" (Abrams, 2000). This mechanism is present if, for example, the searching effectiveness of the predator depends upon both traits but with a certain degree of plasticity, so that the same effectiveness can be achieved for a continuum of pairs (u, v). Since the half saturation constant h is inversely related to searching effectiveness, $h(u, v)$ must be minimum when u and v are balanced, i.e. $u = v$ provided both traits are measured on an appropriate scale. These are standard assumptions for predator-prey community modelling (Abrams, 2000), which have the advantage of involving the minimum possible number of demographic parameters. In our analyses we use (Section A3 in Appendix):

$$K(u) = K_0 \frac{2}{\left(\frac{u}{u_0}\right)^2 + \left(\frac{u_0}{u}\right)^2} \qquad d(v) = d_0 \frac{\left(\frac{v}{v_0}\right)^2 + \left(\frac{v_0}{v}\right)^2}{2} \qquad h(u,v) = h_0 + h_1(u-v)^2 \tag{5}$$

The trait space (u, v) can be partitioned into the three regions $\mathcal{E}$, $\mathcal{S}$, and $\mathcal{C}$ previously described (Section A4 in Appendix). At the boundary between $\mathcal{S}$ and $\mathcal{C}$ all quantities associated with the asymptotic regime of the slow-fast system are discontinuous.

In conclusion, taking into account that the prey birth rate is density-independent, the canonical equation (2) can be specified for the two populations as follows

$$\dot{u} = k^u \langle x \rangle \langle s^u \rangle \tag{6}$$

$$\dot{v} = k^v \left\langle \left(b + \frac{eax}{h+x} \right) y \right\rangle \left\langle \frac{s^v}{b + \dfrac{eax}{h+x}} \right\rangle \tag{7}$$

where superscripts u and v are used to indicate the corresponding species. Of course, the selection derivatives s^u and s^v must be explicitly computed (Section A5 in Appendix) and the time averages must be performed in order to transform eqs. (6, 7) into standard ordinary differential equations. Moreover, since the time averages are different in the coexistence regions $\mathcal{S}$ and $\mathcal{C}$ of trait space, this operation must be performed twice (Sections A6, A7 in Appendix).

4 Results and discussion

State portraits for the eco-evolutionary model (6, 7) can be constructed by numerical simulations. A typical example is shown in Fig. 2. It contains a small region (dark) where the predator undergoes evolutionary extinction (Matsuda and Abrams, 1994*a*; Ferrière, 2000; Dieckmann and Ferrière, 2004), and two evolutionary attractors: an equilibrium with low trait values and a cycle characterised by high trait values. The two basins of attraction are separated by the stable manifold of the saddle lying in region $\mathcal{C}$. If the ancestral conditions are on the left of this manifold the traits converge to the equilibrium so that, after evolutionary transients, the populations coexist at ecological equilibrium, since the evolutionary equilibrium is in region $\mathcal{S}$. However, for some ancestral conditions, one piece of the evolutionary orbit lies in region $\mathcal{C}$: this means that during the corresponding period of time the populations oscillate along an ecological cycle that slowly drifts on the evolutionary timescale. At evolutionary equilibrium prey evolutionary branching (Geritz et al., 1997, 1998; Dercole et al., 2003) may occur, but will not be investigated here.

Population dynamics associated with evolutionary trajectories in the other basin of attraction are radically different. Indeed, long periods of time characterised by slowly varying populations recurrently alternate with long periods of time during which populations fluctuate on an ecological cycle, as a consequence of the attracting evolutionary cycle being partly in region $\mathcal{S}$ and partly in region $\mathcal{C}$.

Fig. 2 highlights the possibility of coevolution along adaptive ridges, which are segments of the boundary separating cyclic from stationary coexistence. Sliding is a novel type of evolutionary dynamics with important ecological implications: when traits are sliding along an adaptive ridge, prey and predator are poised between stationary and cyclic coexistence, i.e. coevolution drives the populations toward and maintain them at the onset of their most complex dynamic behaviour. How sensitive these phenomena are to parameters is investigated by means of a thorough bifurcation analysis (Section A8 in Appendix). Synthesising the results yields a series of eight statements (the first three are general, while the others are specific of predator-prey systems) that we list hereafter and illustrate with selected state portraits (Fig. 3).

(*i*) *Evolutionary sliding and pseudo-equilibria.* Evolutionary sliding along the boundary separating stationary from cyclic coexistence occurs for many parameter settings. The evolutionary sliding can be temporary (sliding segment) or halt at an evolutionary pseudo-equilibrium. When the adaptive traits are sliding, or resting at a pseudo-equilibrium, the populations are in critically stable ecological states and their mean characteristics (densities, density-dependent parameters) can vary abruptly for small changes of individual traits.

(*ii*) *Evolutionary extinction.* There is always a subregion (dark in all state portraits) where the orbits tend toward the boundary of region $\mathcal{E}$. This causes the predator to go extinct in the long run, a phenomenon that is not predictable on the basis of purely ecological arguments. Evolution to extinction had been noted in predator-prey and competition models by Matsuda and Abrams (1994*a*,*b*); Dieckmann et al. (1995), and is also known to occur in models of mutualistic (Ferrière et al., 2002) and cannibalistic (Dercole and Rinaldi, 2002; Dercole, 2003) interactions. These examples highlight a common mechanism. Adaptive evolution is driven by the “marginal” benefit of performing better in interactions (predation, mutualism) than other conspecifics; yet the “direct”, physiological cost to the individual can become so great that eventually the population growth rate becomes negative, causing extinction.

(*iii*) *Multiple evolutionary equilibria.* The eco-evolutionary system most often possesses several equilibria: attractors, repellors and saddles, in addition to predator evolutionary extinction. Two general implications can be drawn. First, in the long run, the same populations can reach different evolutionary states and develop different ecological dynamics due to to ancient differences in their genotypic state. Experimental evolution in *Escherichia coli* provides strong empirical support to this prediction (Travisano et al., 1995). Second, the co-occurrence of predator evolutionary extinction and other viable evolutionary attractors provides a firm mathematical basis for the notion of evolutionary trapping suggested from empirical observations (Colas et al., 1997; Schlaepfler et al., 2002): under given environmental conditions, the predator population can be trapped on an evolutionary trajectory heading to extinction whereas alternative, ecologically safe evolutionary attractors could have been reached. Schlaepfler et al. (2002) and Ferrière et al. (2004) have discussed the implications of evolutionary trapping in a conservation perspective.

(*iv*) *Two forms of Red Queen dynamics.* The first one (evolutionary cycle in region $\mathcal{S}$, see portraits B and A′) corresponds to slow periodic variations of the traits entraining slow population cycles. This form is well-known from Lotka-Volterra models that did not allow for other forms of Red Queen dynamics (Abrams, 2000). The second form (evolutionary cycle in region $\mathcal{S}$ and $\mathcal{C}$, see portraits C and B′) corresponds to slow periodic variations of the traits accompanied by recurrent and long bouts of ecological oscillations. This complex pattern was predicted by Khibnik and Kondrashov (1997) who have named it "eco-genetically driven Red Queen dynamics".

(*v*) *Factors enhancing Red Queen dynamics.* Our study confirms that a bidirectional axis of prey vulnerability is a potent mechanism for generating evolutionary cycles (Abrams, 2000). By increasing the impact of the traits on vulnerability the evolutionary attractor changes in a typical sequence (see portraits A, B, C): first an equilibrium associated with steady populations, then an evolutionary cycle with entrained population oscillations, and finally an evolutionary cycle associated with recurrent bouts of ecological oscillations. For a further increase of the vulnerability mechanism Red Queen dynamics suddenly disappear (see portraits D), a phenomenon that has gone unnoticed in previous studies. Increasing the probability of prey mutation, the variance of the distribution of prey mutational effects, and the maximum predation rate can also trigger and enhance Red Queen dynamics (see portraits (A, A′) and (B, B′)).

(*vi*) *The predator chases the prey.* All evolutionary cycles we have detected are counterclockwise. Thus, the predator trait increases when the prey trait is large and decreases in the opposite case. This results from the bidirectional axis of prey vulnerability, and is, indeed, present in all studies where the prey has a most vulnerable phenotype depending upon predator's trait (see Marrow et al., 1992; Dieckmann et al., 1995; Dieckmann and Law, 1996; Abrams and Matsuda, 1997; Khibnik and Kondrashov, 1997).

(*vii*) *Evolution toward ecological stability: The paradox of enrichment.* Ecological theory predicts that predator-prey interactions should cause large amplitude cycles in rich environments (Rosenzweig, 1971). The "paradox of enrichment" emphasises that this does not occur in nature (e.g. Murdoch et al., 1998). Abrams and Walters (1996) found an ecological solution to the paradox for certain types of predator-prey communities, later confirmed by experimental findings (McCauley et al., 1999). Rosenzweig and Schaffer (1978) took a general, evolutionary approach to the problem, arguing that evolution should tend to restore ecological stability lost through enrichment. Evolution may actually play such a significant role in light of e.g. Yoshida et al.'s (2003) findings on rapid evolutionary change in predator-prey systems. Our work substantiates, refines, and broadens Rosenzweig and Schaffer's view in the case of slow predator and fast prey. In fact, if the system is at its evolutionary equilibrium in region $\mathcal{S}$ (portrait D), would evolutionary processes be absent (i.e. u and v being kept frozen), significant enrichment would destabilise the populations. This is clearly recognisable from portrait D$'$ where the point $*$ in region $\mathcal{C}$ is the copy of the evolutionary equilibrium of portrait D. Interestingly, after enrichment the evolutionary processes act in the opposite direction and the final result (portrait D$'$) is that the traits tend to an evolutionary pseudo-equilibrium. In other words, the full destabilisation of the populations triggered by enrichment is opposed by the counteracting forces of evolution.

(*viii*) *Evolution opposes permanent ecological oscillations.* There seems to be no realistic environmental conditions under which an evolutionary attractor is entirely in region $\mathcal{C}$, although evolutionary trajectories are often trapped on the boundary between $\mathcal{S}$ and $\mathcal{C}$ (see statement (*i*)). Only if the predation rate is almost independent of prey and predator traits (i.e. if h_1 is of the order of 10^{-3}), there is an evolutionary equilibrium in $\mathcal{C}$ (notice that for $h_1 = 0$, point (u_0, v_0) is a stable evolutionary equilibrium in $\mathcal{C}$). Thus, evolution seems to oppose permanent ecological oscillations.

5 Concluding comments

Our analysis unravels novel evolutionary phenomena whose scope extends beyond predator-prey coevolution. This includes the possibility that coevolution guides the traits along adaptive ridges formed by segments of the boundary between the regions of stationary and cyclic coexistence (evolutionary sliding), or comes to a halt at special points of that boundary (evolutionary pseudo-equilibria).

Our conclusions for predator-prey coevolution are likely to be influenced by the specific model chosen to describe the interaction. The analysis, however, should in principle be repeatable for any ecological model involving slow-fast dynamics. Considering the dual case of slow prey (e.g. plants) and fast predator (e.g. insects), and how common recurrent insect-pest outbreaks are in natural or exploited forests, coevolution might well in this case have just the opposite effect on ecological dynamics, namely that of favouring cyclic coexistence.

Finally, the conjecture formulated by Ellner and Turchin on the basis of their analyses of population time series (Ellner and Turchin, 1995), namely that "ecosystems might evolve toward the edge of chaos", finds some support in the present study. Indeed, our findings suggest that ecosystems might evolve toward the edge of their most complex dynamic regime, which in the case of predator-prey models, is indeed cyclic coexistence. But the support could become even stronger once the present analysis is extended to tritrophic food chains with potentially chaotic ecological dynamics. This should be feasible since singular cycles and singular bifurcations responsible for chaotic dynamics have already been found in such communities (De Feo and Rinaldi, 1998). Bifurcations leading to chaos are a likely cause of discontinuity in fitness across trait space. Complex Red Queen dynamics involving intermittent bouts of chaotic fluctuations of the populations would then rank among the expected outcomes, as predicted by Ellner and Turchin (1995).

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Figure captions

Figure 1

Evolution of the traits in the neighbourhood of the boundary separating stationary coexistence (region $\mathcal{S}$) from cyclic coexistence (region $\mathcal{C}$). A, evolutionary sliding toward T (solid boundary) and crossing (dotted boundary). B, evolutionary sliding toward the pseudo-equilibrium P.

Figure 2

A state portrait of the eco-evolutionary model (6, 7). There are three equilibria (a stable node (filled dot) and an unstable focus (empty dot) in region $\mathcal{S}$ and a saddle in region $\mathcal{C}$) and one limit cycle (partly in region $\mathcal{S}$ and partly in region $\mathcal{C}$). There are two attractors, the node and the cycle, and their basins of attraction are separated by the stable manifold of the saddle. There are three sliding segments, one stable (T_1T_2, stretched and magnified in the lower right panel) and two unstable (T_3T_4 and T_5T_6). Predator evolutionary extinction occurs in the dark region. Parameter values: $k^u = 0.1$, $k^v = 1$, $r = 1$, $K_0 = 1$, $h_0 = 0.02$, $h_1 = 0.02$, $d_0 = 0.01$, $b = 0.001$, $e = 0.1$, $a = 5$, $u_0 = 1$, $v_0 = 3$.

Figure 3

Eight state portraits of the eco-evolutionary model (6, 7). In the first row the parameters are $k^u = 0.1$, $k^v = 1$, $r = 1$, $K_0 = 1$, $h_0 = 0.02$, $d_0 = 0.01$, $b = 0.001$, $e = 0.1$, $a = 1.5$, $u_0 = 1$, $v_0 = 3$, and $h_1 = 0.01$ in A, $h_1 = 0.017$ in B, $h_1 = 0.03$ in C, $h_1 = 0.05$ in D. State portrait A$'$ is obtained from A by increasing k^u from 0.1 to 0.145. State portrait B$'$ is obtained from B by increasing a from 1.5 to 3. State portrait C$'$ is obtained from C by increasing v_0 from 3 to 3.3. State portrait D$'$ is obtained from D by increasing K_0 from 1 to 5. All dark regions correspond to predator evolutionary extinction. Evolutionary sliding is present in all panels, while pseudo-equilibria (squared points) are present in panels A, A$'$, B, D$'$.

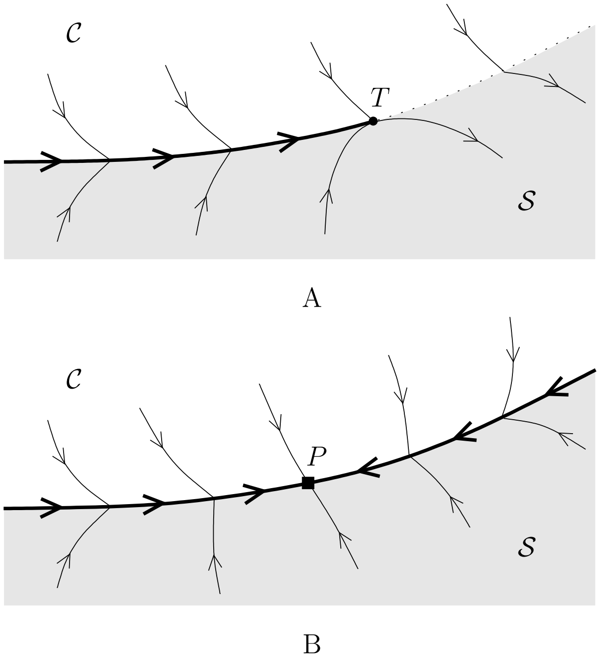

Figure 1

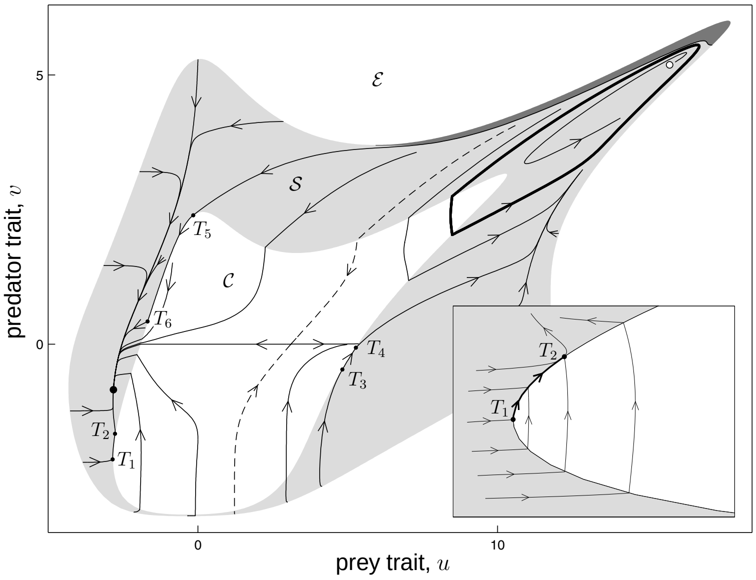
5
0
predator trait, v
0
10
prey trait, u
$\mathcal{E}$
$\mathcal{S}$
$\mathcal{C}$
T_5
T_6
T_4
T_3
T_2
T_1
T_2
T_1

Figure 2

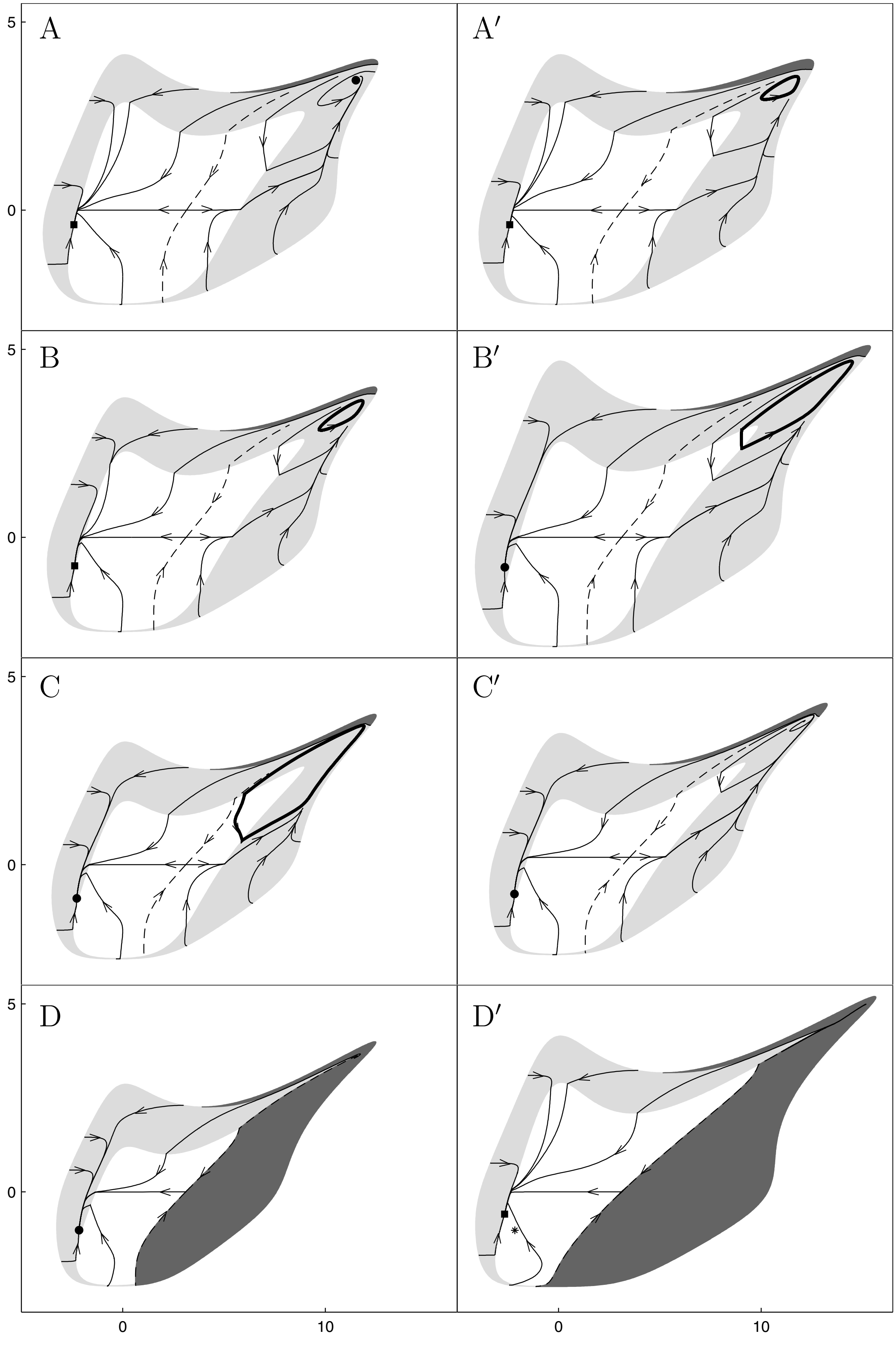

Figure 3

Electronic Appendix

In this appendix we report all modelling assumptions, mathematical details, numerical approximations, and relevant references used in our analysis. Some statements and formulas presented in the paper are repeated here in order to obtain a self-contained presentation of our analysis that could be read without going back and forth between the paper and the appendix. Equations are numbered as (A1), (A2),… and when they correspond to a specific equation mentioned in the paper, this is explicitly pointed out.

A1 The ecological model

The ecological community we consider is a predator-prey interaction described by the standard Rosenzweig-Mac Arthur model (Rosenzweig and MacArthur, 1963)

$$\dot{x}(t) = x(t)\left[r\left(1 - \frac{x(t)}{K}\right) - \frac{ay(t)}{h + x(t)}\right] \tag{A1}$$

$$\dot{y}(t) = y(t)\left[b + e\frac{ax(t)}{h + x(t)} - d\right] \tag{A2}$$

(eqs. (3.1) and (3.2) in paper), where $x(t)$ and $y(t)$ are prey and predator population densities at time t. In the absence of predator, the prey population grows logistically (with intrinsic growth rate r and carrying capacity K), while, in the absence of prey, the predator population decays exponentially (we assume that the intrinsic birth rate b is smaller than the death rate d but that the maximum birth rate $(b + ea)$ is greater than d). Moreover, predators have a Holling type II functional response (with maximum predation rate a and half-saturation constant h) and extra natality resulting from predation is simply proportional to the predation rate through an efficiency coefficient e.

For any parameter setting, model (A1, A2) has a global attractor in the positive quadrant. If the prey carrying capacity is low, i.e.

$$K < \frac{h(d-b)}{ea - d + b} \tag{A3}$$

the attractor is the equilibrium $(K, 0)$, i.e. the predator population goes extinct. In contrast, if the prey carrying capacity is such that

$$\frac{h(d-b)}{ea - d + b} < K < \frac{h(ea + d - b)}{ea - d + b} \tag{A4}$$

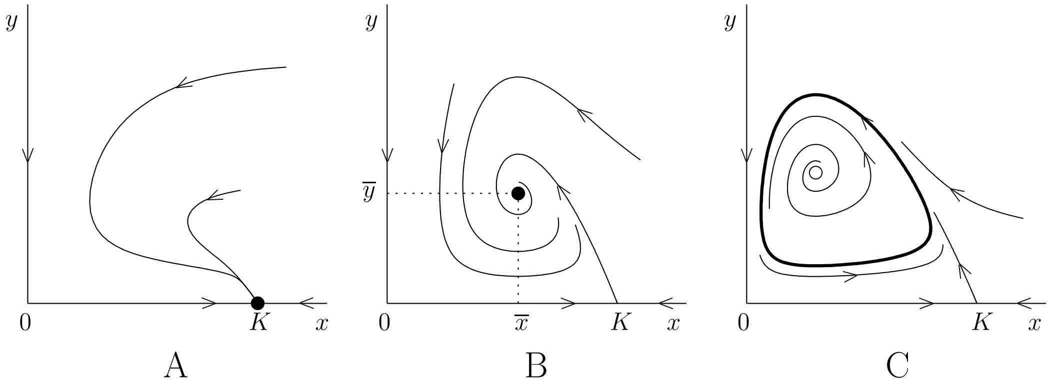

Figure A1: The three state portraits of model (A1, A2): A, predator extinction (see eq. (A3)); B, stationary coexistence (see eq. (A4)); C, cyclic coexistence (see eq. (A6)).

stationary coexistence occurs at the equilibrium

$$\bar{x} = \frac{h(d-b)}{ea-d+b} \qquad \bar{y} = \frac{r}{a}\left(1-\frac{\bar{x}}{K}\right)(h+\bar{x}) \tag{A5}$$

while for high values of K, i.e.

$$K > \frac{h(ea+d-b)}{ea-d+b} \tag{A6}$$

populations coexist on a limit cycle, as shown in Fig. A1. When eq. (A6) is satisfied with the equality sign, i.e. when the vertical predator isocline ($x = (d-b)h/(b+ea-d)$) is passing through the vertex of the non-trivial prey isocline (the parabola $y = r/a\,(1-x/K)\,(h+x)$, see Fig. A2), the equilibrium $(\bar{x}, \bar{y})$ given by eq. (A5) is critically stable and the populations are balanced between stationary and cyclic coexistence. The limit cycle is not known analytically, and this implies that the evolutionary dynamics can not be described explicitly when the prey carrying capacity is high.

A2 The case of slow predator and fast prey

If prey grow at a much faster rate than predators, the limit cycle can be fairly well approximated by the so-called singular limit cycle, which can be easily derived from the isoclines, as shown in Fig. A2. The singular cycle is composed of two fast and two slow phases. The first fast motion is the collapse of the prey population: it occurs when the predator abundance is at its highest value $y_{\max}$. Then, in the absence of prey, predator abundance slowly decays from $y_{\max}$ until a lower threshold $y_{\min}$ is reached. At this point, the prey population rises quickly to $x_{\max}$ while predator abundance remains at its lowest value. Finally, the second slow motion takes place: the predator slowly regenerates and the prey slowly decays along the non-trivial

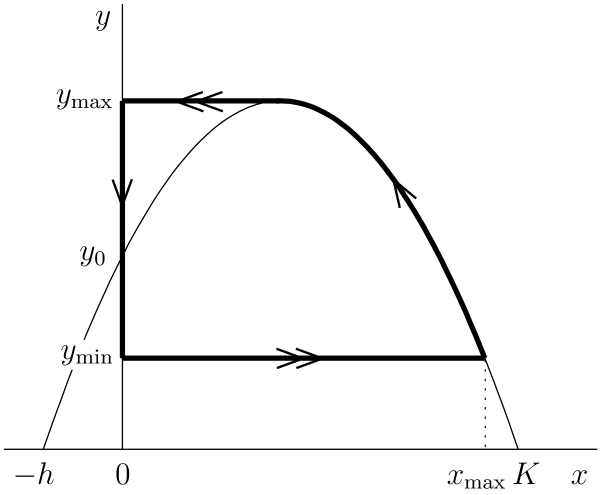

Figure A2: Non-trivial prey isocline (parabola) and singular limit cycle; single [double] arrows indicate slow [fast] motion.

prey isocline (the parabola in the figure).

The maximum predator abundance $y_{\max}$ (the y coordinate of the vertex of the parabola) is given by

$$y_{\max} = \frac{r(K+h)^2}{4aK} \tag{A7}$$

while it can be shown (Rinaldi and Muratori, 1992) that the minimum predator abundance $y_{\min}$ is the solution of the following transcendental equation

$$y_{\max} - y_{\min} = y_0 \log \frac{y_{\max}}{y_{\min}} \tag{A8}$$

where $y_0 = hr/a$ is the intersection of the prey isocline with the vertical axis (see Fig. A2).

A3 Dependence of demographic parameters upon adaptive traits

We now denote by u for the prey, and v for the predator, two species-specific adaptive traits which control the predator-prey interactions. We assume that the prey has density- and trait-independent birth rate, while its death rate has a density-dependent component controlled by u. Thus, r is constant while K depends on u. We further assume that K peaks at u_0, for which the prey is most effective. Similarly, we assume that the predator death rate d depends upon v and is minimum at the trait value v_0, at which predator are best adapted to their environment. Finally, we assume that the predation rate is a function of both traits, and that predator [prey] are favoured [unfavoured] when traits are balanced, i.e. when u and v are in a

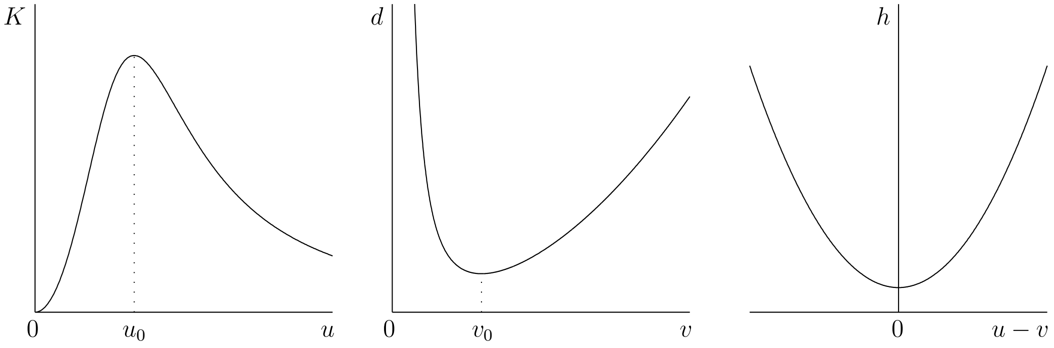

Figure A3: Dependence of the parameters K, d and h upon the prey's and predator's adaptive traits u and v.

suitable relationship, which defines the so-called bidirectional axis of prey vulnerability (Abrams, 2000). This mechanism is present if, for example, the searching effectiveness of the predator depends upon both traits but with a certain degree of plasticity, so that the same effectiveness can be achieved for a continuum of pairs (u, v). Since the half saturation constant h is inversely related to searching effectiveness, the result is that the function $h(u, v)$ is minimum when u and v are balanced. For notational convenience we assume that the traits are measured on a scale such that they balance for $u = v$. In conclusion, we will concentrate on the dependence of the following triplet of demographic parameters upon the traits

$$K = K(u) \quad d = d(v) \quad h = h(u, v) \tag{A9}$$

where K is maximum at u_0, d is minimum at v_0, and h is minimum both with respect to u and v for $u = v$. Our assumption on the relationships between traits and demographic parameters is by no means more meaningful than others from a biological point of view. However, it has the advantage of involving the minimum possible number of demographic parameters. The functions K, d and h used in the following for performing simulations and bifurcation analyses are (see Fig. A3):

$$K(u) = K_0 \frac{2}{\left(\frac{u}{u_0}\right)^2 + \left(\frac{u_0}{u}\right)^2} \quad d(v) = d_0 \frac{\left(\frac{v}{v_0}\right)^2 + \left(\frac{v_0}{v}\right)^2}{2} \quad h(u, v) = h_0 + h_1(u - v)^2 \tag{A10}$$

(eq. (3.3) in paper). Although these functions do not have a specific empirical underpinning, they satisfy all the requirements we have just discussed, they are smooth and can be easily changed by varying their parameters (two for each function).

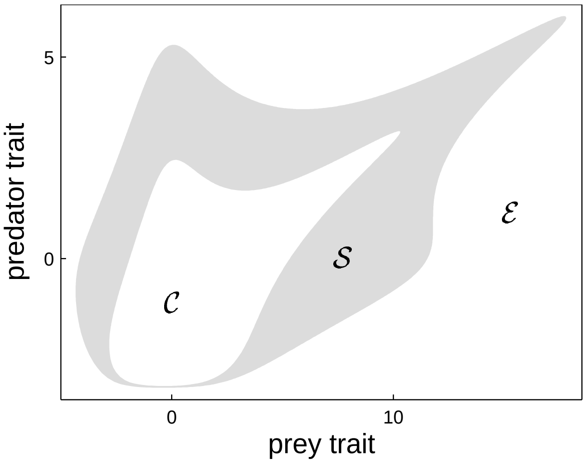

Figure A4: Regions $\mathcal{E}$, $\mathcal{S}$ (grey region), and $\mathcal{C}$, in the trait space (u, v); for $(u, v) \in \mathcal{E}$ the predator population goes extinct (see eq. (A3) and Fig. A1A); for $(u, v) \in \mathcal{S}$ the attractor of model (A1, A2) is an equilibrium (stationary coexistence, see eq. (A4) and Fig. A1B); for $(u, v) \in \mathcal{C}$ the attractor is a limit cycle (cyclic coexistence, see eq. (A6) and Fig. A1C); the figure has been obtained for the following parameter setting: $K_0 = 1$, $h_0 = 0.02$, $h_1 = 0.02$, $d_0 = 0.01$, $b = 0.001$, $ea = 0.5$, $u_0 = 1$, $v_0 = 3$.

A4 Regions of stationary and cyclic coexistence in trait space

Given the possible asymptotic regimes of model (A1, A2), we can immediately infer that the space (u, v) of the traits can be partitioned into three regions $\mathcal{E}$, $\mathcal{S}$, and $\mathcal{C}$ characterised by inequalities (A3), (A4), and (A6), respectively. For traits in region $\mathcal{E}$ the predator population can not persist on ecological timescale, while for traits in regions $\mathcal{S}$ (called stationary coexistence region) and $\mathcal{C}$ (called cyclic coexistence region) the populations persist in stationary or cyclic conditions, respectively. Fig. A4 shows an example of the three regions for the particular parameter setting indicated in the caption. For other parameter settings some of these three regions can disappear or become unbounded. Notice that a nonlinear transformation of the traits appear on the axis of Fig. A4, under which the point (u_0, v_0) becomes the origin.

At the boundary separating region $\mathcal{S}$ from region $\mathcal{C}$ all quantities associated with the asymptotic regime of the slow-fast system are discontinuous. In fact, close to the boundary in region $\mathcal{S}$ the vertical predator isocline is on the right of the vertex of the prey isocline but close to it. Thus, the asymptotic regime is stationary and the equilibrium $(\bar{x}, \bar{y})$ given by eq. (A5) is characterised by a value of $\bar{y}$ very close to $y_{\max}$. By contrast, for pairs (u, v) close to the boundary in region $\mathcal{C}$ the attractor of the slow-fast system is well approximated by the singular limit cycle shown in Fig. A2 which is characterised by a mean value of the predator population much lower than $y_{\max}$ (De Feo and Rinaldi, 1997). This means that an abrupt loss of the mean predator population will accompany any evolutionary transition from region $\mathcal{S}$ to region $\mathcal{C}$, while a sharp increase will occur when evolution proceeds in the opposite direction. Notice that these results are correct for the limit case of complete timescale separation of prey and predator ecological dynamics. However, singular perturbation theory (Tikhonov, 1952; Hoppensteadt, 1966, 1974) guarantees that for the general and more realistic case of contrasting (but not separated) timescales, the evolutionary transition from $\mathcal{S}$ to $\mathcal{C}$, though formally continuous, will be associated with a sharp and marked loss of mean predator population.

A5 The the canonical equation of adaptive dynamics

In order to obtain a set of two coupled autonomous ODEs describing the dynamics of the two traits, we follow the approach of adaptive dynamics, centred on the assumption that random mutations are small and occur rarely (Metz et al., 1996; Dieckmann and Law, 1996; Geritz et al., 1997, 1998). This means that the prey [predator] resident population with density x $[y]$ and trait u $[v]$ generates, from time to time, a small mutant population x' $[y']$ with trait u' $[v']$ slightly different from u $[v]$. After the mutation has occurred, the system is composed of three populations, two of which, namely the resident x $[y]$ and the mutant x' $[y']$ are in competition. If the mutant population does not invade, the trait u' $[v']$ is ruled out from the game, while in the opposite case the mutant population grows, at least temporarily. The possibility of a temporary growth of the mutant population followed by its extinction can be excluded in our case, because this would require the existence of multiple attractors of the population model (Dercole et al., 2002), while model (A1, A2) has a single attractor. Thus, only the fate of the resident population after invasion of the mutant remains to be established. In general, this is not always easy to settle. It might be that the resident goes extinct, so that the mutant replaces the former resident and the trait u $[v]$ is replaced, in the end, by u' $[v']$. But it might also be that the resident and the mutant populations achieve stationary or cyclic coexistence. For large classes of models (in particular Lotka-Volterra models), both stationary and cyclic coexistence can be excluded, but in other models coexistence is possible. In our case, if the mutant is the predator, we have two predator populations (the resident and the mutant) competing exploitatively for the same (logistic) resource. Two predators and one prey can coexist on a limit cycle (Koch, 1974; Hsu et al., 1978), but the conditions for cyclic coexistence in the case of slow predator and fast prey are not satisfied if mutations are small (Muratori and Rinaldi, 1989). Therefore, we can conclude that an invading predator replaces the former resident. Finally, as far as prey mutations are concerned, the so-called invasion implies substitution principle (see Dercole and Rinaldi, 2006) generically guarantees that, if the resident populations are at ecological equilibria, an invading prey mutant substitutes the resident population. Thus, if successful mutations are small and occur rarely enough, evolutionary dynamics within each population remain monomorphic and are described by the so-called canonical equation of adaptive dynamics (Dieckmann and Law, 1996):

$$\dot{u} = k^u \langle x \rangle \langle s^u \rangle \tag{A11}$$

$$\dot{v} = k^v \left\langle \left(b + \frac{eax}{h+x} \right) y \right\rangle \left\langle \frac{s^v}{b + \frac{eax}{h+x}} \right\rangle \tag{A12}$$

(eqs. (3.4) and (3.5) in paper), where k^u and k^v are parameters proportional to the probability of mutation in the prey and predator resident populations, and s^u and s^v, called selection derivatives, are the derivatives with respect to mutant's trait of the initial per-capita rate of increase of the prey and predator mutant populations.

In order to transform eqs. (A11, A12) into autonomous ODEs one must first determine the selection derivatives s^u and s^v. After a mutation has occurred in the prey, the resident-mutant model is:

$$\begin{aligned}
\dot{x} &= rx \left(1 - \frac{x}{K(u)} - \frac{x'}{K(u)} C(u,u') \right) - \frac{A(u,v)x}{1 + A(u,v)Hx + A(u',v)Hx'} y \\
\dot{x}' &= rx' \left(1 - \frac{x}{K(u')} C(u',u) - \frac{x'}{K(u')} \right) - \frac{A(u',v)x'}{1 + A(u,v)Hx + A(u',v)Hx'} y \\
\dot{y} &= y \left(b + e \frac{A(u,v)x + A(u',v)x'}{1 + A(u,v)Hx + A(u',v)Hx'} - d(v) \right)
\end{aligned} \tag{A13}$$

where $C(u,u')$ describes prey intra-specific competition ($C(u,u) = 1$) (MacArthur, 1969, 1970; Gatto, 1990), and $A(u,v)$ and H are predator attack rate and handling time, respectively. Using attack rate A and handling time H, instead of maximum predation rate a and half-saturation constant h, is useful for writing the type II functional response when more than one type of prey is available to the predator (Murdoch, 1969; Chesson, 1983). In the case of a single type of prey $A = a/h$ and $H = 1/a$. We assume symmetric intra-specific competition (i.e. $C(u,u') = C(u',u)$) and, in particular, that $C(u,u')$ is an even function of the difference $u - u'$. Analogously, after the mutation has occurred in the predator population, the resident-mutant model is:

$$\begin{aligned}
\dot{x} &= rx \left(1 - \frac{x}{K(u)} \right) - \frac{ax}{h(u,v)+x} y - \frac{ax}{h(u,v')+x} y' \\
\dot{y} &= y \left(b + e \frac{ax}{h(u,v)+x} - d(v) \right) \\
\dot{y}' &= y' \left(b + e \frac{ax}{h(u,v')+x} - d(v') \right)
\end{aligned} \tag{A14}$$

The prey and predator selection derivatives are therefore given by

$$\begin{aligned} s^u &= \frac{\partial}{\partial u'}\left(\frac{\dot{x}'}{x}\right)\Bigg|_{\substack{u'=u\\x'=0}} = \frac{r}{K^2}K_u x + a\frac{h_v}{h}\frac{y}{h+x} \\ s^v &= \frac{\partial}{\partial v'}\left(\frac{\dot{y}'}{y}\right)\Bigg|_{\substack{v'=v\\y'=0}} = -eah_v\frac{x}{(h+x)^2} - d_v \end{aligned} \tag{A15}$$

Notice that due to the above assumptions on the competition function C, its first-order derivative does not appear in the selection derivative for the prey.

In conclusion, equations (A11) and (A12) can be given the form

$$\dot{u} = k^u \langle f_1 \rangle \left(\frac{r}{K^2}K_u \langle f_1 \rangle + a\frac{h_u}{h}\langle f_2 \rangle\right) \tag{A16}$$

$$\dot{v} = k^v d \langle f_3 \rangle \left(-d_v \langle f_4 \rangle - eah_v \langle f_5 \rangle\right) \tag{A17}$$

where K_u, d_v, h_u, h_v are the derivatives with respect to u and v of the triplet K, d, h given by eq. (A10) and $\langle f_i \rangle$, $i = 1, \ldots, 5$, are the average values on the population attractor corresponding to traits (u, v) of the functions

$$f_1 = x \quad f_2 = \frac{y}{h+x} \quad f_3 = y \quad f_4 = \frac{h+x}{bh+(ea+b)x} \quad f_5 = \frac{x}{(ea+b)x^2 + h(ea+2b)x + bh^2} \tag{A18}$$

Exceptions to monomorphic evolutionary dynamics can occur through prey evolutionary branching (Geritz et al., 1997, 1998) only when traits reach an evolutionary equilibrium of the canonical equation (A11, A12). Prey evolutionary branching has been studied in Dercole et al. (2003) but will not be investigated here.

A6 Derivation of the canonical equation in the stationary coexistence region

Each term $\langle f_i \rangle$ in (A18) can be computed in the region of stationary coexistence, i.e. for $(u, v) \in \mathcal{S}$, by replacing x and y with their equilibrium values given by eq. (A5). After some algebra one obtains

$$\langle f_1 \rangle = \frac{h(d-b)}{ea-d+b} \tag{A19}$$

$$\langle f_2 \rangle = \frac{r}{a}\left(1 - \frac{h}{K}\frac{d-b}{ea-d+b}\right) \tag{A20}$$

$$\langle f_3 \rangle = \frac{rh}{a}\left(1 - \frac{h}{K}\frac{d-b}{ea-d+b}\right)\left(1 + \frac{d-b}{ea-d+b}\right) \tag{A21}$$

$$\langle f_4 \rangle = \frac{1}{d} \tag{A22}$$

$$\langle f_5 \rangle = \frac{(d-b)(ea-d+b)}{hde^2a^2} \tag{A23}$$

Thus, the canonical equation in region $\mathcal{S}$ is composed of eqs. (A10, A16, A17, A19–A23).

A7 Derivation of the canonical equation in the cyclic coexistence region

The terms $\langle f_i \rangle$ in the region of cyclic coexistence, i.e. for $(u, v) \in \mathcal{C}$, can be computed through a series of approximations. The computation is performed under the assumption that the prey population has fast dynamics in comparison with the predator population, and that the half-saturation constant is small with respect to the carrying capacity of the prey, i.e. $h/K \ll 1$. Thus, $\langle f_i \rangle$ can be identified with the average value of f_i on the singular limit cycle (see Fig. A2). Since this cycle is composed of two slow and two fast segments, the computation can be limited to the slow segments. More precisely, if the duration of the first slow phase (along the y axis) is T' and the duration of the second slow phase (along the parabola) is T'', we can write

$$\langle f_i \rangle = \frac{1}{T' + T''}\left(\int_0^{T'} f_i \, dt + \int_0^{T''} f_i \, dt\right)$$

where the two integrals are computed along the slow segments of the singular cycle.

Computation of T' and T''

The first slow phase of the singular cycle is characterised by $y(0) = y_{\max}$ and $x(t) = 0$, so that $\dot{y} = (b-d)y$, i.e. $y(t) = y_{\max} \exp(b-d)t$. Since $y(T') = y_{\min}$, we obtain

$$T' = \frac{1}{d-b} \log \frac{y_{\max}}{y_{\min}} \tag{A24}$$

where $y_{\max}$ is given by (A7) and $y_{\min}$ is identified by (A8).

The second slow phase of the singular cycle is characterised by $x \gg h$, since $h \ll K$. Hence, eq. (A2) can be approximated by $\dot{y} = (b + ea - d)y$ which has the solution $y(t) = y_{\min} \exp(b + ea - d)t$, since $y(0) = y_{\min}$. Since $y(T'') = y_{\max}$, we obtain

$$T'' = \frac{1}{ea-d+b} \log \frac{y_{\max}}{y_{\min}} \tag{A25}$$

Computation of $\langle f_1 \rangle$

During the first slow phase of the singular limit cycle the function f_1 is zero (see eq. (A18)). This implies that

$$\langle f_1 \rangle = \frac{1}{T' + T''} \int_0^{T''} x(t)\, dt$$

where the integration must be performed along the parabola, where

$$x(t) = \frac{K - h}{2} + \frac{K}{2} \sqrt{\left(a + \frac{h}{K}\right)^2 - \frac{4a}{rK} y(t)} \tag{A26}$$

$$y(t) = y_{\min} \exp(ea - d + b)t \tag{A27}$$

This integration can be performed explicitly, without introducing any further approximation. Taking eqs. (A24, A25) into account, the result is eq. (A28), with β, γ and the function Φ as in (A33).

Computation of $\langle f_2 \rangle$

From eq. (A18), we can write

$$\langle f_2 \rangle = \frac{1}{T' + T''} \left(\frac{1}{h} \int_0^{T'} y(t)\, dt + \int_0^{T''} \frac{y(t)}{h + x(t)}\, dt \right)$$

In the first integral $y(t) = y_{\max} \exp(b - d)t$, while in the second integral $x(t)$ and $y(t)$ are as in eqs. (A26, A27). If h is neglected with respect to x in the second term, the two integrals can be performed analytically and the result, using eq. (A24, A25), is equation (A29), with α as in (A33).

Computation of $\langle f_3 \rangle$

From eq. (A18) it follows that

$$\langle f_3 \rangle = \frac{1}{T' + T''} \left(\int_0^{T'} y(t)\, dt + \int_0^{T''} y(t)\, dt \right)$$

where in the first integral $y(t) = y_{\max} \exp(b - d)t$, while in the second integral $y(t)$ can be approximated by the exponential function (A27). A straightforward integration gives eq. (A30).

Computation of $\langle f_4 \rangle$

During the first slow phase of the singular limit cycle, f_4 is constant and equal to $1/b$, while during the second slow phase it is approximately constant and equal to $1/(ea+b)$ (see eq. (A18)). Thus,

$$\langle f_4 \rangle = \frac{T'}{T'+T''}\frac{1}{b} + \frac{T''}{T'+T''}\frac{1}{ea+b}$$

from which, taking eq. (A24, A25) into account, eq. (A31) follows.

Computation of $\langle f_5 \rangle$

During the first slow phase of the singular limit cycle, f_5 is zero, while it can be approximated with $1/((ea+b)x)$ during the second slow phase (see eq. (A18)). Hence,

$$\langle f_5 \rangle = \frac{1}{T'+T''}\int_0^{T''} \frac{1}{x(t)}\, dt$$

where $x(t)$ is given by eq. (A26) with $y(t)$ as in eq. (A27). Also this integral can be computed, using classical decomposition techniques, and the result is eq. (A32).

Computation of $y_{\min}$

The extreme values $y_{\max}$ and $y_{\min}$ of predator density along the singular limit cycle are given by eqs. (A7, A8). While eq. (A7) defines $y_{\max}$ explicitly, eq. (A8) is a transcendental equation that can be solved with respect to $y_{\min}$ only numerically. In order to avoid such a computation each time the right-hand side of the canonical equation must be evaluated for different parameter and trait values, we use an approximated formula for $y_{\min}$, obtained by neglecting the terms of order higher than two in the Taylor's expansion

$$\exp\frac{y_{\min}}{y_0} = 1 + \frac{y_{\min}}{y_0} + \frac{1}{2}\left(\frac{y_{\min}}{y_0}\right)^2 + O\left(\left(\frac{y_{\min}}{y_0}\right)^3\right)$$

The corresponding approximated, but explicit, formula for $(y_{\max} - y_{\min})$ is given in eq. (A33). Of course, the approximation is good if $y_{\min} \ll y_0$, which can be shown to be always the case for $h \ll K$.

Validity of the approximations

All the approximations we have introduced are a priori justified if $h \ll K$. In order to evaluate to which extent our approximations are valid we have systematically compared the values of $\langle f_i \rangle$, $i = 1, \ldots, 5$, given by eq. (A28–A33), with the true values computed through numerical integration of the function f_i along the singular cycle. The result of this analysis, carried out for many parameter settings, is that the approximation is definitely satisfactory for $\langle f_2 \rangle$,..., $\langle f_5 \rangle$ (errors of the order of 1% if $h/K \leq 0.2$). By contrast, the approximation of $\langle f_1 \rangle$ is more crude but still acceptable ($\leq 1\%$ for $h/K \leq 0.1$). Of course, in order to be sure that the impact of our approximations on the final results is not too heavy we should look at the values of h/K in region $\mathcal{C}$. For this, we can first notice that for a particularly meaningful pair of traits, namely the optimal pair (u_0, v_0), h/K is simply given by (see eq. (A10))

$$\frac{h}{K} = \frac{h_0 + h_1(u_0 - v_0)^2}{K_0}$$

and that this value is definitely low (between 0.05 and 0.1 and exceptionally 0.2) in all the examples considered in the paper. A more meaningful indicator is perhaps the portion of region $\mathcal{C}$ in which $h/K \leq 0.2$. Computed on our state portraits this indicator is quite satisfactory: at 95% of the points $(u, v) \in \mathcal{C}$ the ratio h/K is lower than 0.2.

Conclusions

In conclusion, the final result of our analysis is the following

$$\langle f_1 \rangle = \frac{K(d-b)}{2ea} \left\{ \alpha + \frac{hr}{a} \frac{\beta \left[\Phi(-\beta) - \Phi(\beta) \right] - 2\gamma}{y_{\max} - y_{\min}} \right\} \tag{A28}$$

$$\langle f_2 \rangle = \frac{r(ea-d+b)}{ea^2} + \frac{hr^2(d-b)}{ea^3(y_{\max} - y_{\min})} \left[\gamma + \alpha \Phi(\alpha) \right] \tag{A29}$$

$$\langle f_3 \rangle = \frac{hr}{a} \tag{A30}$$

$$\langle f_4 \rangle = \frac{ea-d+2b}{b(ea+b)} \tag{A31}$$

$$\langle f_5 \rangle = \frac{r(d-b)}{ea^2(y_{\max} - y_{\min})(ea+b)} \left[\alpha \Phi(\alpha) + \frac{h}{K} \Phi(-\beta) - \Phi(\beta) \right] \tag{A32}$$

where α, β, γ, and the functions Φ and $(y_{\max} - y_{\min})$ are given by

$$\alpha = 1 - \frac{h}{K} \quad \beta = 1 + \frac{h}{K} \quad \gamma = \sqrt{\frac{4a}{rK}(y_{\max} - y_{\min})} \quad \Phi(w) = \log\frac{w}{\gamma + w}$$
$$y_{\max} - y_{\min} = \frac{r(h+K)^2}{4aK} - \frac{hr}{a}(\rho - \sqrt{\rho^2 - 2}) \quad \rho = \frac{\exp\left(\dfrac{(h+K)^2}{4hK}\right)}{\dfrac{(h+K)^2}{4hK}} - 1 \tag{A33}$$

To sum up, the canonical equation in region $\mathcal{C}$ is approximated by eqs. (A10, A16, A17, A28–A33).

A8 Bifurcation analysis of the canonical equation

The canonical equation (A16, A17) is formally a discontinuous piecewise smooth autonomous dynamical system, also called *Filippov system* (Filippov, 1964, 1988), namely a set of ODEs whose right-hand side is smooth in regions $\mathcal{S}$ (see eqs. (A19–A23)) and $\mathcal{C}$ (eqs. (A28–A33)), but discontinuous at the boundary between them. This discontinuity is the origin of the novel phenomena of evolutionary sliding and pseudo-equilibria. Details on the definition and computation of sliding motions can be found in Filippov (1988) who has been the leading authority in this field since the early sixties.

The most obvious way of studying the canonical equation (A16, A17) is through simulation. For this, after fixing the parameter values, one must simply specify the ancestral conditions, namely the initial values of the traits $(u(0), v(0))$ in the region of coexistence $\mathcal{S} \cup \mathcal{C}$, and then integrate forward in time. The trajectory starting at $(u(0), v(0))$ tends either toward region $\mathcal{E}$, thus revealing a case of predator evolutionary extinction, or toward an attractor in the region of stationary and/or cyclic coexistence. If the ancestral conditions are changed, a new evolutionary path is obtained and the fate of the two populations along this path might be different from the previous one because the canonical equation, being nonlinear, can have multiple attractors. Repeating this process for a sufficiently high number of initial conditions, one obtains a state portrait, namely a set of trajectories in the space (u, v) that fully describes the dynamics of the traits. Moreover, if the two coexistence regions $\mathcal{S}$ and $\mathcal{C}$ are reported in the same diagram, then basic qualitative informations on population dynamics can also be identified.

In order to keep the number of simulations under control and still arrive to some meaningful conclusion about the influence of various parameters on the eco-evolutionary dynamics, one is forced to study the canonical equation, at least to a certain extent, through bifurcation analysis (Kuznetsov, 1998). This means that all the invariant sets of the state portrait (e.g. equilibria and limit cycles, as well as pseudo-equilibria and sliding segments) must be “continued” with respect to a parameter by means of some suitable software (we used SlideCont (Dercole and Kuznetsov, 2005), Auto (Doedel et al., 1997), and Content (Kuznetsov and Levitin, 1997)), in order to detect the critical values of the parameter at which they undergo a bifurcation, i.e. a structural change.

The bifurcation analysis of the canonical equation is much more complex than that of a standard dynamical system, because Filippov systems, besides having all standard bifurcations, have also special bifurcations involving some sliding on the discontinuity boundary (for this reason called *sliding bifurcations*). The simplest example is the appearance or disappearance of a sliding segment, a structural change which can be continued with respect to two parameters. In other words, the points in a two parameter space associated with the appearance of a sliding segment lie on a curve that can be produced through numerical continuation. Another example of sliding bifurcation is the collision of an equilibrium with the discontinuity boundary. Under suitable conditions, this bifurcation gives rise to a pseudo-equilibrium.

The list of the sliding bifurcations is very long and actually known only in the special case of second order systems (Kuznetsov et al., 2003). The use of numerical bifurcation analysis is really mandatory, because the bifurcations and attractors involved in our study are far too many to allow one to reach a useful synthesis only through simulation. However, the presentation of the bifurcation analysis is out of the scope of the present paper. It would require a deep knowledge of sliding bifurcations, a topic that has only recently been touched in the literature.

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