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Research article

Effects of evolution on niche displacement and emergent population properties, a discussion on optimality

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Understanding the effects of evolution on emergent population properties such as intrinsic growth rates, species abundances or resilience is not only a key theoretical question, but has major empirical implications, for instance in conservation, agroecology and invasion ecology. Evolution can also lead to polymorphism based on niche differentiation among different phenotypes. The present article has three aims. First, we clarify the evolutionary scenarios allowing for optimization of population growth rate and abundance. Second, we relate the eco-evolutionary emergence of polymorphism to the niche-overlap and fitness-ratio sensu coexistence theory. Third, we discuss whether properties of polymorphic populations can be optimized due to niche-displacement among phenotypes. We revisit previous theoretical results on eco-evolutionary optimization and link them with our Lotka–Volterra framework. Depending on how the traits under selection affect species intrinsic growth rates or ecological interactions, we uncover three scenarios, ranging from the optimization of all three properties to no optimization and link evolutionary dynamics to coexistence theory. Optimization is, in general, incompatible with niche differentiation sensu coexistence theory and, therefore, with the emergence of polymorphism. Niche displacement between resident and mutant phenotypes, and potentially polymorphism, only arise when we do not expect optimality to hold. Finally, we show how our approach can be generalized to coevolutionary scenarios. In the discussion, we propose biological scenarios and traits that may fall into our three scenarios. Although it is possible to find traits for which optimality is expected, for the majority of the cases optimization arguments do not hold. We also provide practical applications of our results in conservation, agroecology, harvesting and invasion ecology.

Keywords: adaptive dynamics, branching point, coexistence theory, *K*-selection, life history traits, polymorphism

Introduction

Recently, empirical results have accumulated, suggesting that evolution can often impact the dynamics of ecological systems, even on short timescales (Hairston et al.

2005). As a result, we may have to account for such evolutionary phenomena to properly predict or manage the effects of current global changes (Carroll et al. 2014, Urban et al. 2016), to manage exploited species (Allendorf et al. 2008) or agricultural systems (Hendry et al. 2011, Loeuille et al. 2013). Understanding the ecological consequences of evolution requires a non-trivial change in scale, from genes and individuals to populations and ecosystems. Natural selection builds on differences in fitness components of different genotypes. How such individual-level differences scale up to influence the fate of populations is already quite a difficult question. While evolution may enhance population persistence by fostering adaptation (e.g. evolutionary rescue, Gomulkiewicz and Holt 1995), it may also lead to the fixation of traits that decrease population size or even lead to extinctions (Webb 2003). Eco-evolutionary dynamics also alter ecological properties at even larger scales, affecting community structure (e.g. competitive hierarchies, De Meester et al. 2002) and ecosystem functioning (e.g. the strength of trophic cascades and nutrient recycling processes, Loeuille and Loreau 2004, Bassar et al. 2010).

Evolution has often been construed as positive for the evolving population. Statements on evolution happening 'for the good of the species' have been common, giving the impression that evolution optimizes various aspects of population properties (e.g. its abundance or productivity). Many models in evolutionary biology support this view. This may come from a strong focus on adaptation compared to other evolutionary processes, and from the fact that frequency dependence is often disregarded. As explained in Dieckmann and Ferrière (2004), many quantitative genetic models are based on ad-hoc fitness functions that ignore frequency-dependent selection and such too simplistic models often lead to an evolutionary outcome that optimizes intrinsic growth rate r or reproduction ratio R_0. Similar ideas of optimization have also been proposed at even larger scales, from ecosystems, where some works have proposed evolution toward optimal states (Odum and Barrett 1971), even at very large scales (Lovelock and Margulis 1974, Lenton 1998). In recent years, however, several works have shown that evolution only rarely optimizes systems at any of these scales. Dieckmann and Ferrière (2004) discuss how frequency dependence naturally emerges from the ecological context and will most often lead to evolutionary outcomes that do not optimize population characteristics. Mylius and Diekmann (1995) are the first, to our knowledge, showing that depending on how the frequency and density dependence act on the invasion fitness, evolution could optimize the basic reproductive number R_0 or the intrinsic growth rate r. Metz and collaborators (Metz et al. 2008, Metz and Geritz 2016, Lion and Metz 2018) formalized this theory and provided necessary and sufficient conditions for evolution to optimize based on the decomposition of the invasion fitness into traits and environmental variation (see corollary 3.4 in Metz and Geritz 2016).

To better understand the link between evolution and various ecological properties, one possibility is to understand the variations in the mean phenotype, and to explicitly account for their impacts on the ecological dynamics. Evolution can also lead to character displacement within the population and to the long-term maintenance of polymorphisms (Doebeli and Dieckmann 2000, Leimar 2005). Considering the mean phenotype is then no longer relevant. As character displacement occurs, due to disruptive selection, different phenotypes exploit different niches. This not only limits competition and related losses, but also leads to higher complementarity in resource use. These two components can act in synergy to allow higher abundances or productivity to be reached. Therefore, when niche displacement occurs, we expect some population characteristics to be positively affected, as competition is relaxed.

The optimization principle developed by Metz and collaborators (Metz et al. 2008, Metz and Geritz 2016, Lion and Metz 2018) is a general mathematical theorem determining the form of the invasion fitness such that evolution optimizes a population property (their theorem is a necessary and sufficient condition). Now, it remains unclear how these mathematical conditions translate into which biological traits can be expected to lead to optimization or non-optimization and which population property is optimized or not. In this article, we aim at revisiting the optimization principle within the concrete ecological dynamics given by the Lotka–Volterra formalism. Moreover, a corollary of the optimization principle is that optimization is incompatible with the maintenance of polymorphism (Metz et al. 2008, Metz and Geritz 2016, Lion and Metz 2018) and, therefore, typically not associated with biodiversity. From the perspective of coexistence theory (Chesson 1990, Saavedra et al. 2017), the maintenance of biodiversity is constrained by niche overlap and fitness ratio. So, there must be a fundamental link, which still needs to be uncovered, between the optimization/non-optimization and the niche overlap and fitness ratio. Finally, when evolution leads to branching events, niche displacement occurs. While competition should be relaxed, it is unclear whether a population property that is necessarily not-optimized before branching, could be optimized after it because of the niche displacement. We will explain how the optimization principle could be generalized to polymorphism co-evolution.

In this article, we use an explicit Lotka–Volterra model describing ecological dynamics. That is, ecological dynamics are here the results of the intrinsic growth rate and of ecological interactions. In turn, both the intrinsic growth rate and the ecological interactions depend on evolving traits. We start by disentangling scenarios leading to the optimization of the three following emergent population properties: population intrinsic growth rate, its standing abundance and its resilience. We provide a classification into three scenarios, ranging from the optimization of all three properties, optimization of the abundance only and finally non-optimization. Biological traits that would fit the different scenarios are proposed in the discussion. Then, we apply tools of coexistence theory to our three scenarios and relate optimization/non-optimization properties to niche differentiation and fitness ratio (sensu coexistence theory). To demonstrate whether the optimization of a population property occurs, we directly relate the fitness gradient, i.e. the direction of evolution, to the derivative of this population property, i.e. the direction of change in the population properties. This is, we provide a gradient-based approach to the optimization principle of Metz and collaborators (Metz et al. 2008, Metz and Geritz 2016, Lion and Metz 2018). Subsequently, we explain how our findings relate to Metz and collaborators' general mathematical theory. Finally, we explain how our formalism can be used for other emergent properties and explore the co-evolution of two phenotypes after a branching point. From this, we suggest how the optimization principle could be generalized to polymorphism co-evolution, and how it can be proven by a gradient-based approach.

When does evolution optimize emergent population properties?

The first emergent property we study is the intrinsic growth rate r, the per capita growth rate when the population abundance tends to zero. The second is the abundance at equilibrium N^*. The third is resilience (λ) defined as the return rate to equilibrium after small perturbations in abundance. In the polymorphic case resilience is given by the real part of the leading eigenvalue of the Jacobian matrix, while in monomorphic situations it simply reduces to the phenotype intrinsic growth rate. We analyze eco-evolutionary dynamics and optimization using adaptive dynamics techniques, summarized in Box 1.

Scenario 1. Optimization of all three emergent population properties

As a first study case, we consider ecological dynamics following the classical Verhulst model. We assume that only the Malthusian intrinsic growth rate $r(x) > 0$ is a function of the adaptive trait x. Population dynamics of trait x then follow:

$$\frac{dN}{dt} = N \times \left(r\left(x\right) - \alpha \times N\right) \tag{2}$$

where parameter $\alpha > 0$ is the intraspecific competition. In this simple population model, the invasion fitness of a rare mutant x_m in a resident population at ecological equilibrium $N^*(x) = r(x)/\alpha$ is given by

$$\omega\left(x_m, x\right) = r\left(x_m\right) - \alpha \times N^*\left(x\right) \tag{3}$$

We aim at directly relating the direction of evolution (i.e. the fitness gradient $\left(\partial\omega\left(x_m, x\right)\right) / \left(\partial x_m\right)|_{\left(x_m = x\right)}$) to the variations of the abundance ($dN^*(x)/dx$) and of the intrinsic growth rate ($dr(x)/dx$) – our gradient-based approach to the optimization principle. In this first scenario, note that (Supporting information):

Box 1. Adaptive dynamics

In adaptive dynamics, the direction of evolution is determined by variations of the invasion-fitness function $\omega(x_m,x)$, computed as the per capita growth rate of a rare mutant x_m in a resident population x at its ecological equilibrium $N^*(x)$ (Metz et al. 1992, Geritz et al. 1998). The mutant x_m can invade if its invasion fitness is positive. Assuming small mutations, evolutionary changes are then proportional to the fitness gradient assessed at the resident phenotype, and can then be approximated by (Dieckmann and Law 1996):

$$\frac{dx}{dt} = \frac{1}{2}\mu\sigma^2 N^*\left(x\right) \times \frac{\partial\omega\left(x_m, x\right)}{\partial x_m}\Big|_{x_m = x} \tag{1}$$

The term $\mu\sigma^2 N^*(x)$ encapsulates the phenotypic variability brought by the mutation process on which selection acts, as μ corresponds to the per capita mutation rate and σ^2 to the phenotypic variance associated with a mutation event. The last term – the partial derivative of the invasion fitness – defines the fitness gradient that gives the direction of evolution. When the gradient is positive (respectively negative), larger (respectively smaller) values of the trait are selected. Evolutionary singular strategies correspond to the roots of the fitness gradient, i.e. when the gradient is null.
Evolutionary singular strategies can be either convergent (in which case local evolutionary trajectories will converge to the strategy) or divergent (in which case natural selection favours strategies away from the singular strategy). They can also be invasible by nearby mutants, or non-invasible (ESS). Convergence and invasibility of singular strategies can be investigated using the second derivatives of the invasion fitness, assessed at the singularity (Dieckmann and Law 1996, Geritz et al. 1998).
Evolutionary singular strategies that are convergent and non-invasible are called continuously stable strategies (CSS). They correspond to endpoints of evolution. In turn, a strategy that is convergent and invasible defines a branching point and leads to the emergence of polymorphism. Non-convergent strategies correspond to repellor or Garden of Eden (whether they are invasible or non-invasible, respectively), and evolution moves away from those points.

$$\frac{\partial\omega\left(x_m, x\right)}{\partial x_m}\Big|_{x_m = x} = \frac{dr\left(x\right)}{dx} = \alpha \times \frac{dN^*\left(x\right)}{dx} \tag{4}$$

Because singular strategies nullify the fitness gradient (Box 1), Eq. 4 shows that they correspond to local maxima or minima in abundances and intrinsic growth rates (zeros of the intrinsic growth rate and abundance derivative). Outside of equilibria, along evolutionary dynamics, Eq. 4 implies that evolution continuously increases intrinsic growth rates and abundances. Therefore, evolution selects phenotypes with larger intrinsic growth rates, dynamical resilience (which in this case equals the intrinsic growth rate $\lambda(x) = r(x)$) and abundances. CSSs correspond to local maxima in these emergent population properties, while repellors correspond to local minima (proof in the Supporting information).

Figure 1 illustrates this first scenario for two generic intrinsic growth rate functions. (A) and (D) show evolutionary trajectories, while (B) and (E) show corresponding pairwise invasibility plots (PIPs). PIP plots show in grey, for a given resident phenotype on the x-axis, the set of mutant phenotypes, y-axis, that can invade it. They show the positions of evolutionary singularities (at the intersection of the diagonal and the zero fitness contour) and allow to graphically determine whether these strategies are convergent or divergent, invasible or non-invasible (Dieckmann and Law 1996, Geritz et al. 1998). For clarity, we report the direction of evolution determined from the PIP on (C) and (F). (C) and (F) show how the value of phenotype affects emergent ecological properties. In both examples, evolution optimizes all emergent properties. The result applied whether singular strategies exist ((A)–(C)) or not ((D)–(F)). Computations are detailed in the Supporting information.

Scenario 2. Optimization of abundance only

As a second study case, we consider that both the intrinsic growth rate, $r(x) > 0$, and the intraspecific competition $\alpha(x) > 0$ of Verhulst's model depend on phenotype x. The invasion fitness of a rare mutant x_m in a resident population at ecological equilibrium $N^*(x) = r(x)/\alpha(x)$ is given by:

$$\omega(x_m, x) = r(x_m) - \alpha(x_m) \times N^*(x) \qquad (5)$$

As shown in the examples of Fig. 2, evolution no longer optimizes the intrinsic growth rate and the dynamical resilience, but still optimizes the abundance. This is demonstrated following the same rationale as for the first scenario, i.e. trying to relate the fitness gradient to the abundance and the

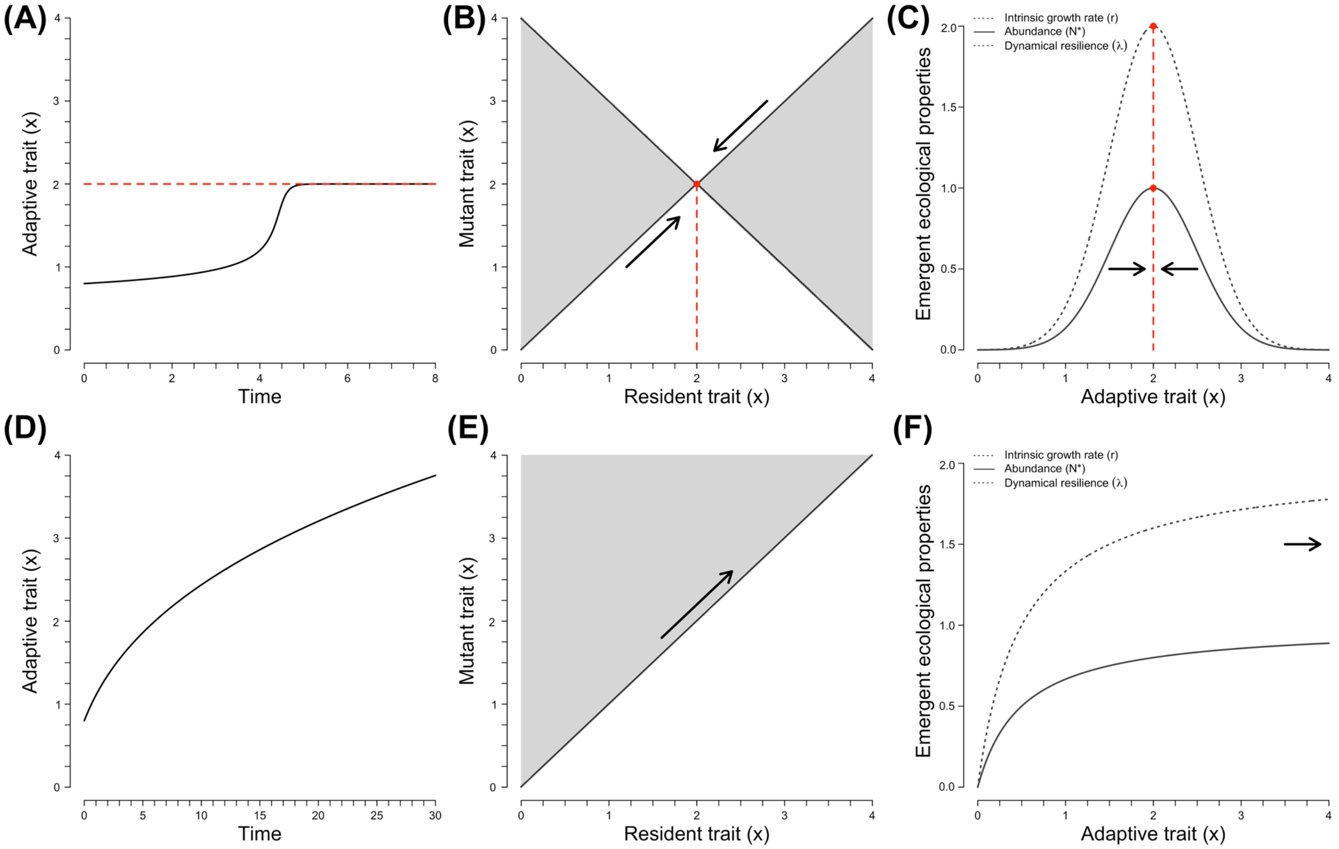

Figure 1. Two examples of eco-evolutionary dynamics leading to the optimization of intrinsic growth rates, abundances and dynamical resilience. (A) and (D) show the evolutionary trajectories, while (B) and (E) show corresponding PIP plots. On a PIP plot the area is grey, if for a given resident phenotype on the x-axis, the set of mutant phenotypes, y-axis, that can invade it. (C) and (F) show how the three emergent ecological properties change along phenotypic variations. Evolutionary singular strategies are in red, and the black horizontal arrows show the direction of evolutionary trajectories. (A)–(C) assume that growth rates $r(x) = r_m \times \exp\left(-\left(x - r_o\right)^2 / \left(2 \times \sigma_r^2\right)\right)$, are optimal when $x = r_o$ (here $r_m = 2$, $r_o = 2$, $\sigma_r = ½$). (D)–(F) assume growth rates to be a monotonically increasing and saturating function of the phenotype $r(x) = r_m \cdot x/(h_r + x)$ ($r_m = 2$, $h_r = 0.5$, $\alpha = 2$).

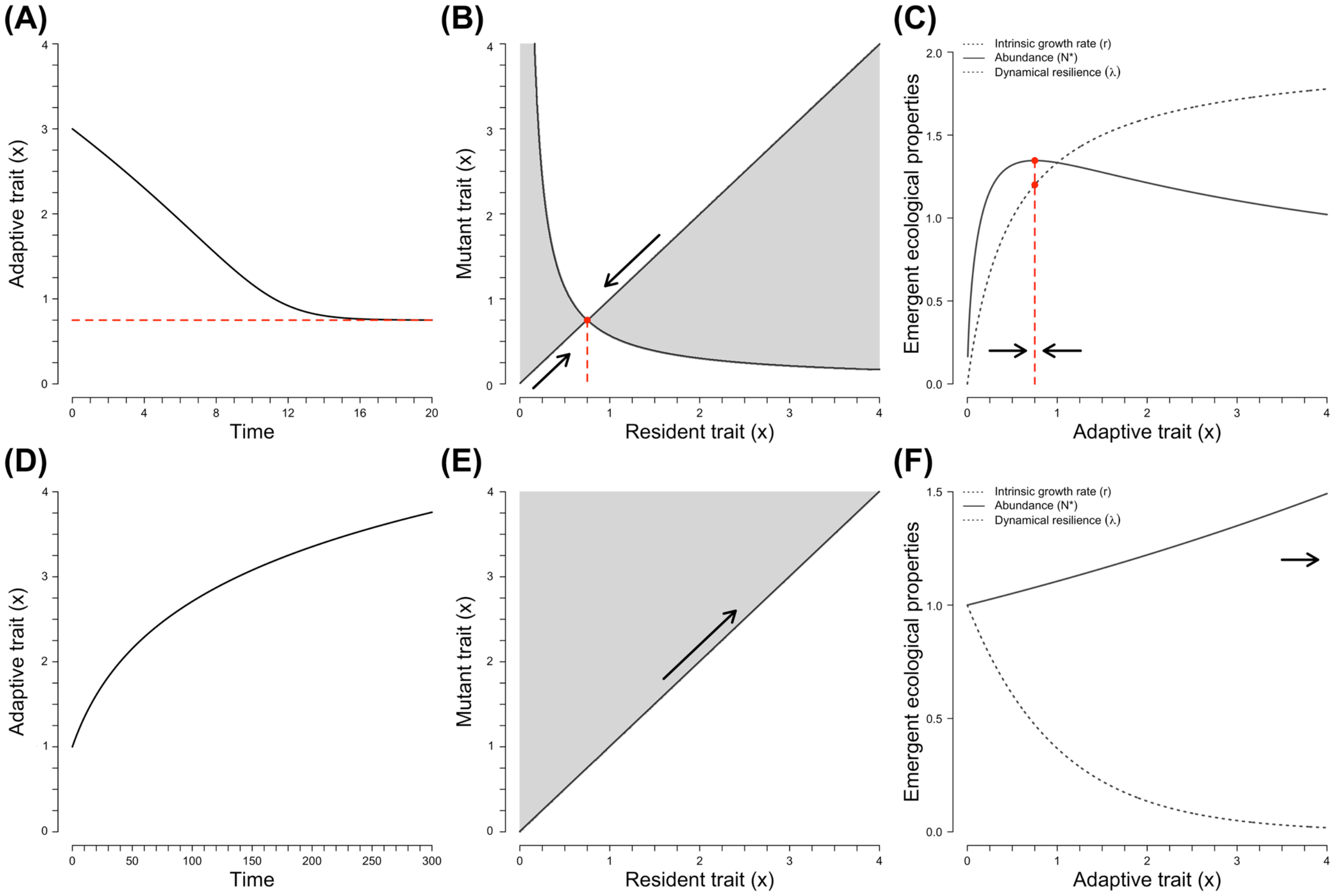

Figure 2. Two examples of eco-evolutionary dynamics leading to the optimization of abundances only. (A) and (D) show the evolutionary trajectories, while (B) and (E) show the corresponding PIP plots. (C) and (F) show how the three emergent ecological properties change along phenotypic variations. Evolutionary singular strategies are in red, and the black horizontal arrows show the direction of evolutionary trajectories. (A)–(C) assume $r(x) = r_m \times x/(h_r + x)$ and $\alpha(x) = \alpha_0 \times x^{\delta}$ ($r_m = 2$, $h_r = 1/2$, $\alpha_o = 1$, $\delta = 0.4$). (D)–(F) assume $r(x) = r_m \times \exp(-\lambda_r x)$ and $\alpha(x) = \alpha_m \times \exp(-\lambda_\alpha x)$ ($r_m = 1$, $\lambda_r = 1$, $\alpha_m = 0$ and $\lambda_\alpha = 1.1$).

intrinsic growth rate derivative. This can be written in two ways (Supporting information):

$$\frac{\partial\omega\left(x_m, x\right)}{\partial x_m}\Big|_{x_m=x} = \frac{dr\left(x\right)}{dx} - \frac{d\alpha\left(x\right)}{dx} \times N^*\left(x\right) \tag{6}$$

or

$$\frac{\partial\omega\left(x_m, x\right)}{\partial x_m}\Big|_{x_m=x} = \alpha\left(x\right) \times \frac{dN^*\left(x\right)}{dx} \tag{7}$$

Equation 6 shows that (unless $d\alpha(x)/dx = 0$ for all x, which would be in contradiction with our assumption that $\alpha(x)$ is a function of x) evolution does not optimize intrinsic growth rate (and dynamical resilience). The second equality (Eq. 7) demonstrates that evolution still selects phenotypes with larger equilibrium abundances. As in the first study case, we can further demonstrate that singular strategies can only be convergent and non-invasible (CSS) or divergent and invasible (a repellor). Again, CSSs correspond to local maxima in population abundances, while repellors correspond to local minima (proof in the Supporting information).

Figure 2 illustrates this scenario and highlights how evolution optimizes abundances, but not intrinsic growth rates or dynamical resilience. Emergent properties of the system are then traded off along evolutionary dynamics, as it is certainly possible in these situations to get a highly productive system that has a low resilience (e.g. (F)). The argument applies whether singular strategies exist ((A)–(C)) or not ((D)–(F)). Mathematical details are provided in the Supporting information.

Scenario 3. Non-optimisation

We now consider that the competition strength between mutants and residents depends on both traits x and x_m, i.e. $\alpha(x_m,x)$ for the competitive effect of a resident x on a mutant x_m. Therefore, the invasion fitness of a rare mutant x_m in a resident population at ecological equilibrium $N^*(x) = r(x)/\alpha(x,x)$ is given by

$$\omega\left(x_m, x\right) = r\left(x_m\right) - \alpha\left(x_m, x\right) \times N^*\left(x\right) \tag{8}$$

We now get (Supporting information):

$$\frac{\partial\omega\left(x_m, x\right)}{\partial x_m}\Big|_{x_m=x} = \frac{dr\left(x\right)}{dx} - \frac{\partial\alpha\left(x_m, x\right)}{\partial x_m}\Big|_{x_m=x} \times N^*\left(x\right) \tag{9}$$

and

$$\frac{\partial\omega\left(x_m, x\right)}{\partial x_m}\Big|_{x_m=x} = \alpha\left(x, x\right) \times \frac{dN^*\left(x\right)}{dx} - \frac{\partial\alpha\left(x_m, x\right)}{\partial x}\Big|_{x_m=x} \times N^*\left(x\right) \tag{10}$$

The first Eq. 9 is similar to Eq. 6 of the second scenario. Excluding the particular case where $\partial\alpha\left(x_m, x\right) / \partial x_m \,|_{x_m=x} = 0$ for all x, evolution no longer favours larger intrinsic growth rates (and dynamical resilience). Given the second equality (Eq. 10), unless we are in the particular case that $\partial\alpha\left(x_m, x\right) / \partial x \,|_{x_m=x} = 0$ for all x, evolution does not optimize abundance either.

Figure 3 illustrates this case, assuming that phenotypes compete asymmetrically for resources (as in Kisdi 1999). Depending on parameter values, the system can reach a CSS ((A)–(C)) or an evolutionary branching ((D) and (F)) (Kisdi 1999). Whether the singular strategy (red dot) is a CSS or a branching can be visualized on the PIP plots ((B) and (E)). In (B), above and below the red dot the area is white, meaning that the mutant phenotype cannot invade, which implies a CSS. In contrast in (E), the area above and below the red dot is grey, so that nearby mutants can invade, which implies a branching point (Geritz et al. 1998). Consistent with the previous analysis (Eq. 9 and 10), none of the population properties are maximized. Computations of evolutionary singular strategies, their convergence and invasibility properties are given in Kisdi (1999).

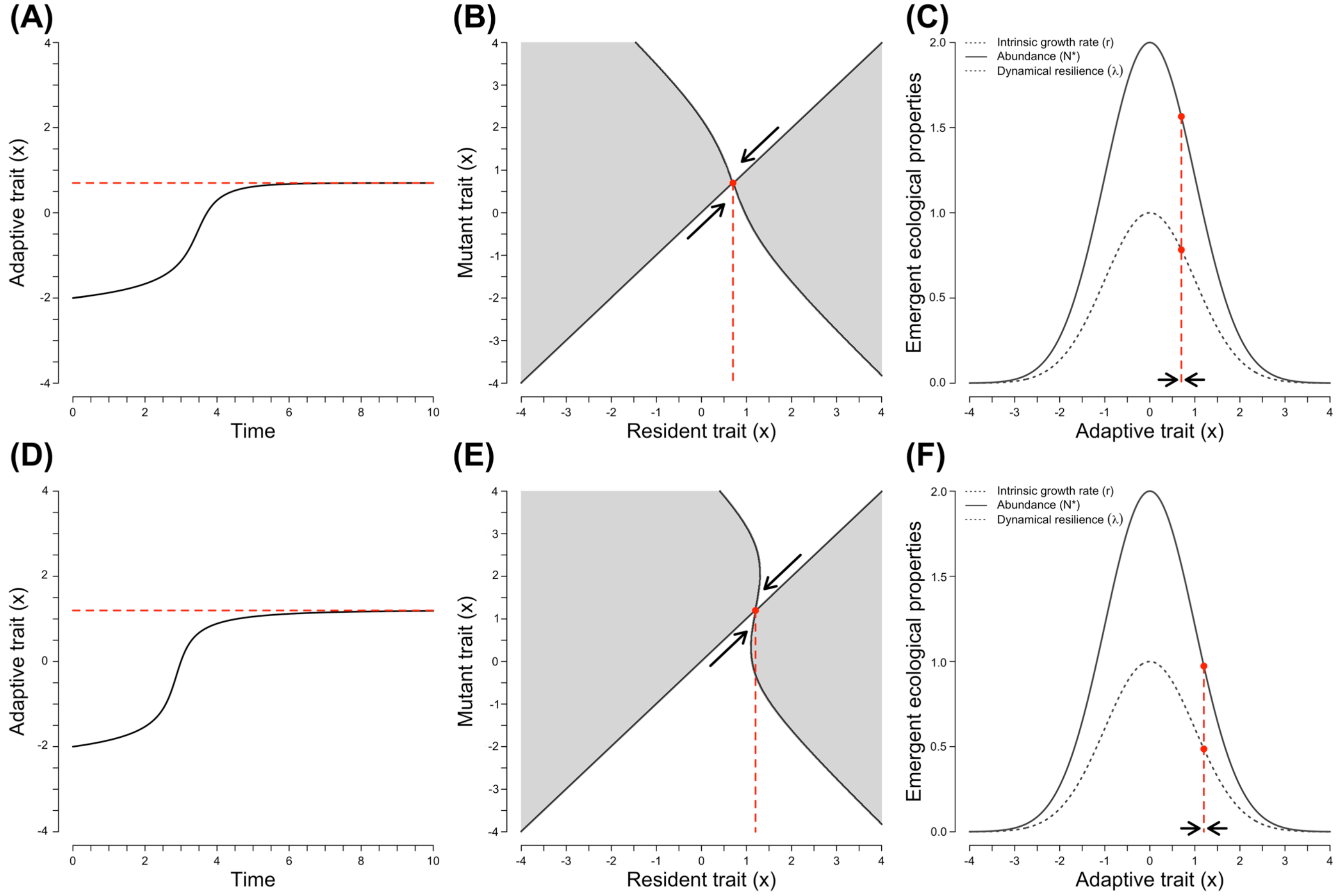

Figure 3. Two examples of eco-evolutionary dynamics illustrating the non-optimisation of abundances, intrinsic growth rate and dynamical resilience. (A) and (D) show the evolutionary trajectories, while (B) and (E) show the corresponding PIP plots. (C) and (F) show how the three emergent ecological properties change along phenotypic variations. Evolutionary singular strategies are in red, and the black horizontal arrows show the direction of evolutionary trajectories. The competition model is given by: $r\left(x\right) = r_m \times \exp\left(-\left(x - r_o\right)^2 / 2\sigma_r^2\right)$ and the competition between two phenotypes x and y is given by $\alpha\left(x, y\right) = c \times \left(1 - 1/\left(1 + \nu \times \exp\left(-k \times \left(x - y\right)\right)\right)\right)$, so that competition is asymmetric, favouring higher phenotypic values (Kisdi 1999). (A)–(C) assume $r_m = 1$, $r_o = 0$, $\sigma_r = 1$, $c = 1$, $k = 1.4$ and $\nu = 1$; while (D)–(F) assume $r_m = 1$, $r_o = 0$, $\sigma_r = 1$, $c = 1$, $k = 2.4$ and $\nu = 1$. Note that evolutionary dynamics in (D) will eventually lead to branching (shown on Fig. 4A).

Contrary to the previous two scenarios, convergence and invasibility are not simply related. Instead, all types of singular strategies are possible, in particular branching points. At such branching points, disruptive selection leads to the emergence of polymorphism (Fig. 3D–F). In such cases, trait displacement occurs among individuals of the population, niche differentiation (sensu the coexistence theory) between two coevolving phenotypes progressively appears, and the system eventually settles at a coalition of two CSSs (Kisdi 1999). Such a divergence decreases competition between increasingly contrasted phenotypes (limiting similarity, see MacArthur and Levins 1967). This will be studied in 'Polymorphism coevolution after branching' section.

Relating evolutionary dynamics to coexistence theory

We now investigate the link between the evolutionary outcomes of these three scenarios and coexistence theory. From an ecological perspective, the resident-mutant dynamics can be considered as a special case of classical models of two competing species. Following the framework of coexistence theory, niche-overlap (ρ) and fitness-ratio (κ) metrics between the two phenotypes can then be assessed (Chesson 1990, Saavedra et al. 2017). Noting r_i the intrinsic growth rate of phenotype i and $\alpha_{i,j}$ the competitive effect of j on i, we get:

$$\rho = \sqrt{\frac{\alpha_{m,r}\alpha_{r,m}}{\alpha_{r,r}\alpha_{m,m}}} \text{ and } \kappa = \frac{r_r}{r_m}\sqrt{\frac{\alpha_{m,m}\alpha_{m,r}}{\alpha_{r,r}\alpha_{r,m}}} \tag{11}$$

As detailed below, in our two first scenarios, Eq. 11 leads to $\rho = 1$, indicating a full niche overlap (no niche difference). The mutant then fails invading if $\kappa > 1$, while it replaces the resident if $\kappa < 1$. In the more general case (third scenario), we get $\rho < 1$. This indicates that overlap is now imperfect, i.e. a certain degree of niche differentiation. The mutant and the resident phenotypes can coexist provided that:

$$\frac{1}{\rho} > \kappa > \rho \tag{12}$$

If the first inequality fails, the resident excludes the mutant, while if the second inequality fails the mutant replaces the resident.

Consequently, coexistence theory implies that if there is no niche difference between the resident and the mutant ($\rho = 1$), coexistence between both phenotypes and, therefore, emergence and maintenance of polymorphism (through evolutionary branching) is not possible. Given niche differentiation ($\rho < 1$), the two phenotypes can potentially coexist and, therefore, a branching point is possible.

In the first scenario, interactions among residents and mutants do not depend on traits so that $\alpha_{i,j} = \alpha$ and $\rho = 1$. Therefore, either the mutant replaces the resident or fails to invade depending on κ. As $K = r(x)/r(x_m)$, evolution systematically selects mutants with larger intrinsic growth rates (and higher abundances since $N^*(x) = r(x)/\alpha$, and higher resilience as $\lambda(x) = r(x)$).

In the second scenario, interactions among resident and mutant $\alpha_{i,j}$ depend on phenotype i so that $\alpha_{r,m} = \alpha_{r,r} = \alpha(x)$ and $\alpha_{m,r} = \alpha_{m,m} = \alpha(x_m)$. Again $\rho = 1$, either the mutant replaces the resident or it fails to invade. Fitness difference now equals $K = r(x)/r(x_m) \times \alpha(x_m)/\alpha(x) = N^*(x)/N^*(x_m)$. Consequently, evolution selects mutants with larger abundances, i.e. evolution optimizes N^* only, but has no systematic effect on the intrinsic growth rate and resilience.

In the third scenario, the niche overlap is given by

$$\rho = \sqrt{\frac{\alpha\left(x_m, x\right)\alpha\left(x, x_m\right)}{\alpha\left(x, x\right)\alpha\left(x_m, x_m\right)}} \tag{13}$$

When $\rho < 1$, meaning that competition among similar phenotypes is higher than between different phenotypes, coexistence is possible (as long as the inequalities (Eq. 12) are satisfied), hence the maintenance of polymorphism. Moreover, the fitness ratio is given by

$$\begin{aligned} \kappa &= \frac{r\left(x\right)}{r(x_m)} \times \sqrt{\frac{\alpha\left(x_m, x_m\right)\alpha\left(x_m, x\right)}{\alpha\left(x, x\right)\alpha\left(x, x_m\right)}} \\ &= \frac{N^*\left(x\right)}{N^*\left(x_m\right)} \times \sqrt{\frac{\alpha\left(x, x\right)\alpha\left(x_m, x\right)}{\alpha\left(x, x_m\right)\alpha\left(x_m, x_m\right)}} \end{aligned} \tag{14}$$

which implies that evolution will not necessarily increase abundances or intrinsic growth rates, as selection of larger abundances or larger intrinsic growth rates can be countered by the imbalance in competition, i.e, the square root terms in Eq. 14.

In summary, there is a fundamental ecological difference between the first two scenarios and the third one. The first two scenarios, implicitly assume no niche differentiation ($\rho = 1$) between the resident and the mutant phenotypes, while in the third scenario, competition has been defined such that niche differentiation occurs ($\rho < 1$) competition being a function of the traits of the two interacting populations. Consequently, in the first two scenarios, evolution cannot lead to a branching point. The mutant and the resident phenotypes cannot coexist for lack of niche differentiation. In the third scenario a branching point could occur. Niche differentiation is then a necessary condition, but not sufficient to obtain a branching. Constraints on fitness ratios (Eq. 12) should also be satisfied. Finally, in the case of no niche differentiation, the fitness ratio reveals which phenotype is selected by evolution. In scenario 1 it is the phenotype with the larger abundance and intrinsic growth rate, while in scenario 2, it is the phenotype with larger abundance that is selected.

Polymorphism coevolution after branching

Figure 3D–F show that when competition depends on both the mutant and the resident trait ($\alpha(x_m,x)$), a branching point can be possible. After this branching point, Fig. 4 and 5 show that two phenotypes coexist and coevolve.

Figure 4 shows how coevolution affects the three emergent properties we consider. (A) shows, as expected, the progressive niche separation between the two phenotypes, therefore a reduction of their competition. (B)–(D) explore whether the three emergent population properties are optimized after the branching. As the niches of the two phenotypes diverge, total abundance (C) and dynamical resilience (D) both increase, but do not reach their potential maximum. The intrinsic growth rates of both phenotypes diverge, but the average growth rate remains approximately constant (panel B).

On Fig. 5A and C, the coloured areas define the protected dimorphism area (i.e. in these areas, phenotypes 2 can grow when rare in an equilibrium population of phenotype 1 and vice versa). Ecologically, these areas correspond to pairs of phenotypes that coexist (Kisdi 1999). These two panels show that neither the total abundance nor the dynamical resilience is optimized after the branching. In coexistence theory, these protected dimorphism areas can be represented in the fitness-ratio (κ) and niche-overlap (ρ) space (see Fig. 2 of Chesson 1990) using Eq. 11 with $x_r = x_1$ and $x_m = x_2$ (Supporting information). The grey area on (B) is the projection of the protected dimorphism area in the fitness-ratio (κ) and niche-overlap (ρ) space given the constraint $1/\rho > \kappa > \rho$ (Eq. 12). This panel shows that coevolution decreases niche overlap, but interestingly, the two phenotypes remain equivalent from a fitness point of view ($\kappa = 1$).

How our results relate to the optimization principles of Metz and collaborators

We now link our gradient-based approach to the mathematical theorem of Metz and collaborators (Metz et al. 2008, Metz and Geritz 2016, Lion and Metz 2018). Following

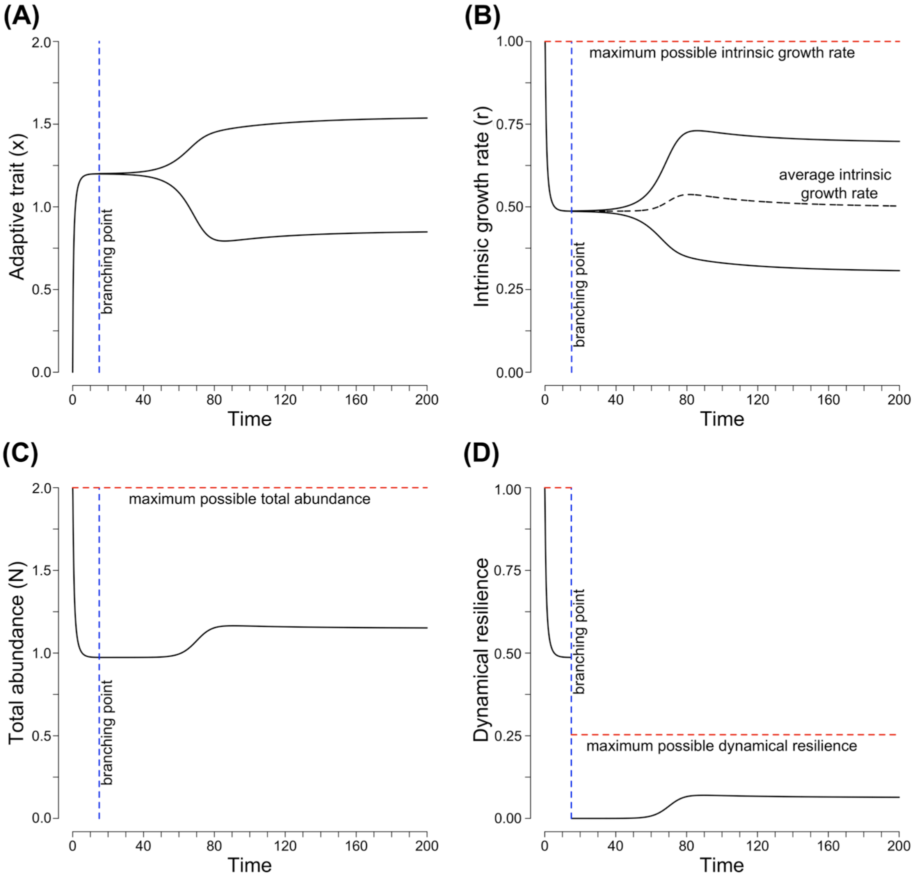

Figure 4. Co-evolutionary trajectories past the branching point of Fig. 3D–F. (A) shows the coevolution of the phenotypic traits, it is the continuation of Fig. 3 D. (B)–(D) show how evolution affects the intrinsic growth rates, the total abundance and the dynamical resilience, respectively. On all panels, the vertical blue dashed lines represent the time of the branching process. On (B)–(D), the horizontal red dashed lines give the potential maximum value of the corresponding emergent properties, i.e. the maximum value that could be reached if one could choose the value of the phenotypes arbitrarily. On (B), the black dashed line shows how evolution affects the average intrinsic growth rate. On (D), the maximum possible dynamical resilience is calculated as the maximum over all pairs of trait values allowing coexistence.

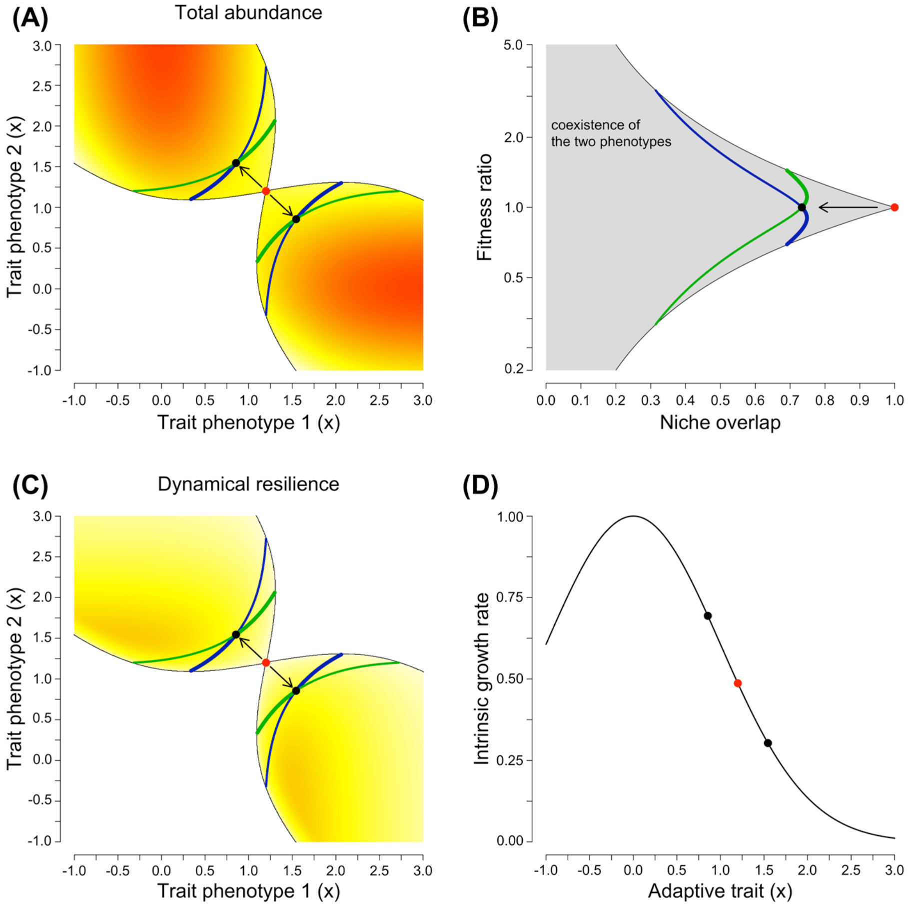

Figure 5. Coevolution of the two phenotypes after the branching point of Fig. 3D–F (Fig. 4). The red dot shows the branching point, while the black dots show the coalition of phenotypes to which the system converges. Green and blue lines correspond to the coevolutionary isoclines, i.e. the set of points at which evolutionary gradients equal zero for phenotype 1 and of phenotype 2, respectively. These two isoclines can be either invasible or non-invasible, depending on the sign of the second derivatives of the relative fitness functions. Thick lines show non-invasible strategies, while thin lines indicate invasibility. (A) and (C) show the effects of evolution on abundance and resilience. The coloured area corresponds to the protected dimorphic area. The colour gradient on (A) gives the total abundance of the two phenotypes at ecological equilibrium, while on (C) it stands for the dynamical resilience. (B) shows changes in the fitness-ratio (κ) and niche-overlap (ρ) for the two phenotypes along coevolutionary dynamics. (D) shows how coevolution affects intrinsic growth rates.

Metz and Geritz (2016), optimization is expected if and only if the invasion fitness can be written as:

$$\omega\left(x, x_m\right) = f\left(x, x_m\right) \times \left(\psi\left(x_m\right) - \psi\left(x\right)\right) \tag{15}$$

with f a function taking only positive values and ψ a function of the trait space in the real numbers. In such cases, because mutants are selected when their invasion fitness is positive, evolution necessarily maximizes ψ (corollary 3.4 in Metz and Geritz (2016)).

In our first scenario, the invasion fitness is $\omega(x_m,x) = r(x_m) - \alpha \times N^*(x)$, which can be rewritten as:

$$\omega\left(x_m, x\right) = r\left(x_m\right) - r\left(x\right) = \alpha \times \left(N^*\left(x_m\right) - N^*\left(x\right)\right) \tag{16}$$

On the first formulation, we recognize Metz's criterion for $\psi = r$ and $f = 1$, and on the second formulation for $\psi = N^*$ and $f = \alpha$. Thus, evolution optimizes r and N^*. The invasion fitness of our second scenario reads as $\omega(x_m,x) = r(x_m) - \alpha(x_m) \times N^*(x)$, which can be rewritten as:

$$\begin{aligned}\omega\left(x_m, x\right) &= r\left(x_m\right) - \frac{\alpha\left(x_m\right)}{\alpha\left(x\right)} \times r\left(x\right) \\ &= \alpha\left(x_m\right) \times \left(N^*\left(x_m\right) - N^*\left(x\right)\right)\end{aligned} \tag{17}$$

Thus, evolution optimizes only N^*, but not r (because of the ratio of the competition term). Finally, the invasion fitness emerging from our third scenario is $\omega(x_m,x) = r(x_m) - \alpha(x_m,x) \times N^*(x)$ which cannot be reformulated following Metz and collaborators (Eq. 15). We can obtain two equivalent formulations, highlighting either r or N^*:

$$\begin{aligned}\omega\left(x_m, x\right) &= r\left(x_m\right) - \frac{\alpha\left(x_m, x\right)}{\alpha\left(x, x\right)} \times r\left(x\right) \\ &= \alpha\left(x_m, x_m\right) \times \left(N^*\left(x_m\right) - \frac{\alpha\left(x_m, x\right)}{\alpha\left(x_m, x_m\right)} \times N^*\left(x\right) \right)\end{aligned} \tag{18}$$

Consider the second expression, (the same rationale applies to the first one). We set f as $f(x,x_m) = \alpha(x_m,x_m)$ and ψ as $\psi = N^*$. The term $\alpha(x_m,x)/\alpha(x_m,x_m)$ remains, which represents the competitive effect of the resident on the mutant relative to the mutant competition on itself. When this ratio does not equal 1, niche differentiation exists and evolution does not optimize N^*. In this sense, we could reinterpret the optimization principle given by Metz's equation (Eq. 15) in the lens of coexistence theory. Optimization holds only if there is no niche differentiation between the resident and the mutant.

Finally, it is also interesting to draw a parallel with the original formulation of the optimization principle (Metz et al. 2008), which states that optimization happens when the resident (assumed to be at its ecological equilibrium and thereby defining the environment) acts uni-dimensionally and monotonically on the invasion fitness of a rare mutant. Such a criterion needs a clear definition of the environment and of its dimensionality, which is not obvious. In the literature, environment is defined as all properties of the resident species, at its ecological equilibrium, that influences the invasion fitness function of a rare mutant. In the first two scenarios, Eq. 16 and 17 clearly show that the resident acts on the invasion fitness through its abundance $N^*(x)$, which is therefore a suitable environment metric. It is clearly unidimensional as N^* is a positive real number, and it acts monotonically on the fitness as an increase (decrease) in $N^*(x)$ implies a decrease (increase) of $\omega(x_m,x)$. In the third scenario (the second row Eq. 18, the trait of the resident acts on the invasion fitness by changing the average abundance $N^*(x)$ defining the competition context for the mutant, but also through changes in $\alpha(x_m,x)$ that modulates this competition effect. Consequently, the environment does not reduce to $N^*(x)$ so that the dimension of the environmental feedback is above one. Durinx et al. (2008) (their appendix E) suggest that such situations can be construed as feedback loops of dimension infinite. Note also that in this case, polymorphism is possible. The relationship between the dimension of the environmental feedback loop, coexistence and branching events has also been pointed (Meszena and Metz 1999). The dimension of the environmental feedback loop offers an upper bound to the total diversity, ie, the number of phenotypes after successive branchings is strictly inferior to this dimension, which is coherent with the results proposed here.

A gradient-based approach to the optimization principle

The aim of this section is to provide a general framework to our gradient-based approach. First, we show how the Eq. 4, 7 and 10 of the three studied scenarios can be framed within a common framework for monomorphic populations. We then explain how it can be generalized to polymorphic coevolution.

In the monomorphic case, we define two classes of invasion fitness function:

$$\text{class I } \omega\left(x_m, x\right) = f^I\left(x_m, P^*\left(x\right)\right) \tag{19}$$

$$\text{class II } \omega\left(x_m, x\right) = f^{II}\left(x_m, x, P^*\left(x\right)\right) \tag{20}$$

where $P^*(x)$ is a real number representing a property of interest of a population of trait x at the ecological equilibrium of the population. In our three scenarios, we used the emergent population properties that are the intrinsic growth rates $r(x)$ and the abundance $N^*(x)$. The main difference between these two classes is the dimension of the environmental feedback loop sensu Metz and collaborators (Metz et al. 2008, Metz and Geritz 2016, Lion and Metz 2018). In class I, the environment feedback, determined by the resident of trait x, is given by its property $P^*(x)$; a single real number for each trait value x. Thus, the feedback is uni-dimensional. In class II, the environment is determined by the property $P^*(x)$ and also by the trait x directly, so that the environmental feedback loop is above dimension one. This is the case in our third scenario, where the interaction is determined by both the resident x and the mutant x_m traits. Note that class I corresponds to the original formulation of invasion fitness functions leading to optimization as defined by Metz and collaborators (Metz et al. 2008). Class II aims at making explicit that the resident phenotype acts on the invasion fitness not only through its abundance, but that its trait value x has also a direct impact, e.g. by changing the interaction strength and by creating niche differences.

For class I, the fitness gradient and the property $P^*(x)$ derivative are directly linked (see Supporting information for details),

$$\frac{\partial \omega\left(x_m, x\right)}{\partial x_m}\Big|_{x_m = x} = -\frac{\partial f^I\left(x, P\right)}{\partial P}\Big|_{P = P^*\left(x\right)} \times \frac{dP^*\left(x\right)}{dx} \tag{21}$$

while for class II we get:

$$\begin{aligned}\frac{\partial \omega\left(x_m, x\right)}{\partial x_m}\Big|_{x_m = x} = &-\frac{\partial f^{II}\left(x, x, P\right)}{\partial P}\Big|_{P = P^*\left(x\right)} \times \frac{dP^*\left(x\right)}{dx} \\ &- \frac{\partial f^{II}\left(x_m, x, N\right)}{\partial x}\Big|_{P = P^*\left(x\right), x_m = x}\end{aligned} \tag{22}$$

For class I, Eq. 21 generalizes Eq. 4 and 7, while for class II Eq. 22 generalizes Eq. 9 and 10. Equation 21 demonstrates that for class I, evolutionary singular strategies (roots of the left term) correspond to local maxima or minima of the property P^*. Furthermore, we can prove that singular strategies are either CSS or repellor (Supporting information). Whether the property P^* is at a local maximum or minimum at the singular strategy depends on the sign of the derivative of f^I. If this sign is negative, the property P^* is maximized, while if it is negative, it is minimized. But as a minimum corresponds to a maximum of $-P^*$, evolution optimizes or pessimizes (up to a choice of sign) if the invasion is of class I for the property P^*. For class II, Eq. 22 contains an extra term, the partial derivative of f^{II} relative to x. This term matches the partial derivative of α on the right side of Eq. 9 and 10. Unless ecological dynamics constrain the partial derivative of f^{II} relative to x in Eq. 22 to be zero, singular strategies do not correspond to local maxima or minima of P^*. Furthermore, we can prove that the cross derivative of the invasion fitness function no longer vanishes in general (Supporting information), so that any type of evolutionary singular strategy is possible.

Utmost it is important to note that class I and class II, for a given system, are not mutually exclusive. For a given property P_1^*, the invasion fitness can be of class I, while for another property P_2^*, it will be of class II. Scenario 2 is an example of such a system; for $P_1^* = N^*$ it is of class I (see first row of Eq. 17), but for $P_2^* = r$ it is of class II (see second row of Eq. 17). Another interesting example is to consider a competition function that is multiplicative separable, i.e. $\alpha(x_m,x) = c(x_m) \times \sigma(x)$. The invasion fitness of this system is of class II for the property $P^* = N^*$ and $P^* = r$, but it is of class I for the property $P^*(x) = \sigma(x) \times N^*(x) = r(x)/c(x)$. That is, evolution optimizes this latest property and branching is not allowed (admittedly, such an emergent property is rarely relevant from an empirical or applied point of view). Consistently, we can prove that the niche overlap sensu coexistence theory is of one ($\rho = 1$), and the fitness ratio is equal $\mathrm{K} = P^*(x)/P^*(x_m)$. Details for this example are given in the Supporting information.

To summarize, for a given system:

1) If there exists a property, such the invasion fitness is of class I. This property is optimized, and branching is impossible.
2) If there exists a property, such the invasion fitness is of class II. This property is in general not optimized, and branching not a priori impossible.
3) Class I and II are not mutually exclusive. That is, it could exist a population property P_1^* such the invasion fitness is of class I and another property P_2^* such that the invasion fitness is of class II. P_1^* is then optimized while P_2^* is in general not optimised, and branching is not allowed (because P_1^* is optimized).

Class I and II of invasion fitness functions can be generalized to polymorphic coevolution or, more generally, to species coevolution as follows. The evolution of each phenotype i (or species) is defined by its invasion fitness $\omega_i(x_{i,m},x)$, i.e. the per capita growth rate (or sign equivalent) of a rare mutant $x_{i,m}$ in a resident community of n phenotypes (or species) $x = (x_1, x_2, \ldots, x_n)$ at ecological equilibrium. We extend class I and class II to polymorphism by

$$\text{class I} - \text{poly } \omega_i\left(x_{i,m}, x\right) = f_i^I\left(x_{i,m}, \boldsymbol{P}^*\left(x\right)\right) \text{ for all phenotypes } i \tag{23}$$

$$\text{class II} - \text{poly } \omega_i\left(x_{i,m}, x\right) = f_i^{II}\left(x_{i,m}, x, \boldsymbol{P}^*\left(x\right)\right) \text{ for all phenotypes } i \tag{24}$$

where $P^* = \left(P_1^*\left(x\right), P_2^*\left(x\right), \cdots, P_n^*\left(x\right)\right)$ is the vector containing the property for each of the n phenotypes. The same conclusions as in the monomorphic case apply. In class I evolution converges to a local maximum or minimum in the population properties, while this is not the case in class II. Moreover, in class I, singular strategies can only be a CSS or a repellor. Cases of polymorphisms have already been discussed in previous works (Metz et al. 2008, Metz and Geritz 2016), where coalitions of n phenotypes are considered, associated with feedback loops of various dimensions (from 1 to many). It is not quite clear how unidimensional feedback loops could lead to such polymorphic situations, as to maintain n phenotypes a feedback loop of dimension at least n is required (Meszena and Metz 1999). In our results, evolution does not necessarily maximize (or minimize) the property that is considered, but our environmental feedback loop is multidimensional. In class I-poly, the environmental feedback loop is the vector of property $\boldsymbol{P}^*$, whose dimension equals the number of phenotypes. Details are given in the Supporting information.

Discussion

Understanding whether evolution leads to optimality in intrinsic growth rate, abundance or resilience is not only a theoretical question, but has practical implications for conservation, for the sustainable management of exploited species, and for invasion biology among others. After a theoretical discussion, we will discuss these empirical implications.

Whether evolution optimizes r (or R_0 often used in epidemiology but first introduced in demography) and/or abundances is a long-standing question. The belief that evolution maximizes population properties is still widespread. Indeed, quite often intrinsic growth rate (or one of its components) or variations in abundance are considered as good proxies to assess the fitness landscape. This, however, ignores the fact that this landscape is dynamic, due to frequency or density dependent selection (Dieckmann and Ferrière 2004). Here, density dependent selection is accounted for as invasion-fitness depends on the resident abundance (or density), as is frequency dependent selection (the fitness of an invading mutant being positive, while it becomes null when it has replaced the resident). It is however not sufficient to introduce frequency and density dependent selection to stay away from r and/or abundance optimization. As shown above, but also in Metz et al. (2008), Metz and Geritz (2016) or Lion and Metz (2018), optimization of r (or R_0) and/or N^* can still be achieved for specific form of invasion fitness.

The evolutionary outcome of the three studies scenarios can be understood based on coexistence theory (Chesson 1990, Saavedra et al. 2017). Importantly, optimization is incompatible with niche differentiation (i.e. niche overlap $\rho < 1$ sensu coexistence theory) between the resident and the mutant phenotypes and therefore incompatible with branching events. In the specific cases (first and second scenarios) where a complete niche overlap exists, the fitness ratio κ then determines whether the mutant can invade, and evolution systematically selects the phenotype with the largest abundance (K-selection) and largest intrinsic growth rate in scenario 1, and the largest abundance in scenario 2. The third scenario often leads to niche differentiation (i.e. $\rho < 1$), so that branching events are possible, while optimization is generally lost for all emergent properties we considered. The tight relationship we observe here between the occurrence of polymorphism and optimality is consistent with previous results concerning the role of evolution in epidemiology (Lion and Metz 2018).

To derive our results, we proposed a new gradient-based approach of the optimization principle. This approach directly links fitness gradients, hence the direction of evolution, to abundance and growth rate derivatives. Our results are completely in line with those obtained by another approach by Metz and collaborators (Metz et al. 2008, Metz and Geritz 2016, Lion and Metz 2018). We show that our gradient-based approach can be extended to polymorphic coevolution, paving the road to a polymorphic optimization principle.

Our distinction of three scenarios of fitness functions naturally raises the question of which biological traits could reasonably fit these different categories. Scenario one requires that the trait only affects the intrinsic growth rate (intrinsic fecundity and mortality) with no direct effect on interaction rates. Phenotypic traits that only affect intrinsic reproduction or survival without clear impact on the ecological niche are logical candidates. Similarly, traits that only incur a tradeoff between basic fecundity and survival (e.g. along the slow–fast continuum, Rose et al. (2009)) could also fall in this category. Evolution of such traits could lead to optimization. Scenario two requires that the trait affects simultaneously the intrinsic growth rate and competitive ability. Some plant defences have been suggested to evolve along this tradeoff (Blossey and Notzold 1995, Agrawal et al. 2012). This class could also include traits that evolve along the $r - K$ continuum (MacArthur and Wilson 1967, Pianka 1970). Their evolution could theoretically lead to the optimization of biomass or density, but not of the other properties we studied. We caution however that for biological traits to fall into the two first scenarios, one has to thoroughly check that additional environmental components are not directly affected by the trait, which may often be difficult to assess. Also, many of the traits that are considered central from an ecological point of view, such as body size or phenology, are presumably interesting because they constrain simultaneously life history and many different interactions. Body size for instance constrains many different life history traits (Peters and Peters 1986), but also competitive hierarchies (Persson et al. 2003) and trophic interactions (Woodward and Hildrew 2002). For such multidimensional traits, especially relevant for the understanding of the structure and functioning of ecological communities, optimization through evolution does not seem to be a reasonable expectation.

Our results suggest that evolution will seldom optimize population growth rates, as this only happens for our first scenario. Because growth rates are here directly linked to resilience, we also found evolution to often be detrimental from a stability point of view. This has important consequences for various management or conservation aspects. In conservation, restoring intrinsic growth rates is a very important objective to prevent or reverse the decline of the rare populations. Evolution is now more often considered in conservation plans (Stockwell et al. 2003). While our results suggest that natural selection will not necessarily help to maximize the growth rate, we still agree that evolution in general and genetic variability in particular should be carefully considered in conservation plans. Indeed, such restorations of variability would alleviate negative effects of genetic drift or inbreeding, aspects that are not explicitly accounted for in our analysis, but likely very important in rare populations. Population growth rate will then be increased, as detrimental mutations will be less easily fixed.

Management of intrinsic growth rates is equally important for invasive species. As these species typically start from a restricted set of individuals, their vast increase in population size or area occupied is in essence a problem of population growth rate. We believe that our results may have several implications in this regard. Fast evolution in various traits has been observed in invasive species (Mooney and Cleland 2001). Whether such an evolution will further increase the growth rate of the species, thereby making possible side effects of the invasion to be larger, is an important matter. Our results suggest that we should not necessarily expect such an outcome. Particularly, fast counterselection of defence traits have repeatedly evolved in invasive species (Müller-Schärer et al. 2004), as these species are often freed from some of their natural enemies ('enemy release hypothesis'). Depending on the tradeoff structure associated with these defence traits, biological situations may be close to optimization or not. When defences only have direct impacts on growth or competitive ability, assuming fixed herbivore densities, optimization of some properties may happen. Because such traits however often directly affect many ecological interactions, they may often follow our third scenario. In such cases, their evolution should not optimize the invasive species' intrinsic growth rate. A similar line of reasoning could be applied to epidemics. Avoiding epidemics largely relies on the control of the infection growth rate (that is, keeping the R_0 below one). As disease agents often have fast generation times and large populations, evolution readily occurs and affects this R_0. Our approach suggests that, except for the most simplified ecological scenarios, such evolution will not optimize the R_0 (see Lion and Metz 2018 for a complete analysis of this topic).

Next to the management of species intrinsic growth rates, understanding the effects of evolution on population density or biomass is equally important. Most food resources consumed by human populations stem from the use of exploited species, wild (e.g. fisheries) or domesticated (e.g. agriculture). The amount of resources is often correlated to the density or biomass available. From an agricultural point of view, humans may guide the evolution of the species directly through artificial selection. Our results highlight that the relationship between the trait that is modified and the ecological interactions of the cultivated species with other species of the ecosystem will largely determine whether optimization can be expected or not. Because the interaction context is often simplified in selection assays, this highlights that many traits that are selected due to optimality in this reduced context may eventually lead to non-optimal phenotypes in the field (Loeuille et al. 2013). Now consider wild species. While direct artificial selection is then not possible, harvesting these species incurs large extra-mortality. Such large selective pressures often yield fast evolution. For instance, in many fished species, evolution to earlier maturity at smaller adult size has been observed (Grift et al. 2003, Olsen et al. 2004). Because body size is involved in many ecological interactions, reviewed by Edeline and Loeuille (2020), we expect its evolution to belong to class II models. Therefore, it is quite possible for this evolution to be detrimental to the standing density or biomass.

Our results also highlight that evolution may readily produce tradeoffs among different emergent properties. Indeed, optimization of all three emergent population properties only occurs in the simplest scenario. In all other instances, any optimality in one of the emergent properties will come at a cost in one of the other. This has important applied consequences. Ecological management is not simply about improving one population aspect, but several ones. Conservation of rare species often aims at improving their growth rates, but also to maintain large enough densities. In the case of fisheries, it is important not only to maintain high abundances (to get a certain yield but also to avoid unwanted ecological consequences such as population crashes), but also to maintain the resilience of the system (Conover and Munch 2002). Given evolution of maturity and body size in harvested species, we expect their evolution to follow class II models. Evolutionary dynamics are unlikely to foster a double objective of high abundances and large resilience. In line with this idea, the evolution of earlier maturity in Newfoundland cod stocks may be one of the reasons for the lack of recovery of the population, and has been directly linked to changes in resilience (Olsen et al. 2004).

To conclude, we propose that, while we have worked here on very simple models in very simplified situations, the topic at hand may have far-reaching implications not only from a conceptual and theoretical point of view, but also affect how we view the conservation and management of natural systems. This is especially true given the fast accumulating evidence that evolution occurs on quite short timescales (Hairston et al. 2005), given current global changes (Urban et al. 2016). Exact implications for more complex systems (e.g. in the case of diffuse coevolution in complex ecological networks) or for specific cases require further investigation, and will certainly bring a new set of exciting questions.

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Author contributions

Rudolf P. Rohr: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal). **Nicolas Loeuille**: Conceptualization (equal); Formal analysis (equal); Investigation (equal); Methodology (equal); Writing – original draft (equal); Writing – review and editing (equal).

Data availability statement

There are no additional data for this paper.

Supporting information

The Supporting information associated with this article is available with the online version.

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Supporting Information: Effects of evolution on niche displacement and emergent population properties, a discussion on optimality

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S1: Mathematical details for the three scenarios

In this appendix, we provide all mathematical details behind the three scenarios we studied in section (2) of the main text.

Mathematical detail for the first scenario

The invasion fitness of the first scenario reads as

$$\omega(x_m, x) = r(x_m) - \alpha \cdot N^*(x). \tag{S1.1}$$

As a consequence, the fitness gradient is given by

$$\left.\frac{\partial \omega(x_m, x)}{\partial x_m}\right|_{x_m=x} = \left.\frac{dr(x_m)}{dx_m}\right|_{x_m=x} = \frac{dr(x)}{dx}. \tag{S1.2}$$

The abundance at ecological equilibrium equals $N^*(x) = r(x)/\alpha$, consequently its derivative relative to x equals

$$\frac{dN^*(x)}{dx} = \frac{1}{\alpha} \cdot \frac{dr(x)}{dx}. \tag{S1.3}$$

Together with equation (S1.2), it proves equation (4) of the main text.

Evolutionary singular strategies can be either convergent (in which case local trajectories will converge to the strategy) or divergent (in which case natural selection favours strategies away from the singular strategy). They can also be invasible by nearby mutants, or non-invasible (ESS). Convergence and invasibility of singular strategies can be investigated using second derivatives of the relative fitness, assessed at the singularity (Dieckmann and Law, 1996). The singularity is convergent if and only if

$$\left.\frac{\partial^2\omega(x_m,x)}{\partial x\partial x_m}\right|_{x_m=x} + \left.\frac{\partial^2\omega(x_m,x)}{\partial x_m^2}\right|_{x_m=x} < 0. \tag{S1.4}$$

The singularity is non invasible if and only if

$$\left.\frac{\partial^2\omega(x_m,x)}{\partial x_m^2}\right|_{x_m=x} < 0. \tag{S1.5}$$

The second partial derivative of the invasion fitness is given by

$$\left.\frac{\partial^2\omega(x_m,x)}{\partial x_m^2}\right|_{x_m=x} = \left.\frac{d^2r(x_m)}{dx_m^2}\right|_{x_m=x} = \frac{dr^2(x)}{dx^2} = \alpha\cdot\frac{d^2N^*(x)}{dx^2}, \tag{S1.6}$$

and the crossed derivative by

$$\left.\frac{\partial^2\omega(x_m,x)}{\partial x_m\partial x}\right|_{x_m=x} = 0. \tag{S1.7}$$

The crossed derivative being always equal to zero implies that singular strategies can only be either 1) convergent and non-invasible, i.e., a CSS, or 2) non-convergent and invasible, i.e., repellor. Moreover, with the second partial derivative, we conclude that the singular strategy is non-invasible (and therefore a CSS) if and only if the intrinsic growth rate (or species abundance) is at a local maximum (negative second derivative). Similarly, the singular strategy is invasible (and therefore a repellor) if and only if the intrinsic growth rate (or species abundance) is at a local minimum (positive second derivative).

Model of fig. 1 panels A to C

The intrinsic growth rate $r(x)$ is given by a bell-shape function of the form

$$r(x) = r_m\cdot e^{-(x-r_o)^2/(2\cdot\sigma_r^2)}. \tag{S1.8}$$

Parameters are r_m the maximum intrinsic growth rate, r_o the optimum value in the trait x, and σ_r the width of the bell-shape curve. Note that $r(x) > 0$ for all trait value x. The fitness gradient equals

$$\left.\frac{\partial \omega(x_m, x)}{\partial x_m}\right|_{x_m=x} = \frac{dr(x)}{dx} = \frac{x - r_o}{\sigma_r^2} \cdot r_m \cdot e^{-(x-r_o)^2/(2\cdot\sigma_r^2)}. \tag{S1.9}$$

Its unique root is $x^* = r_o$. Evolutionary singular strategies match the optimum in intrinsic growth rate $x^* = r_o$. Second and cross derivatives of the relative fitness function, evaluated at the singular strategy x^* are given by

$$\left.\frac{\partial^2 \omega(x_m, x)}{\partial x_m^2}\right|_{x_m=x=x^*} = -\frac{r_o}{\sigma_r^2} \cdot r_m < 0, \tag{S1.10}$$

and

$$\left.\frac{\partial^2 \omega(x_m, x)}{\partial x_m \partial x}\right|_{x_m=x=x^*} = 0. \tag{S1.11}$$

This proves that the singular strategy $x^* = r_o$ is convergent and non-invasible, i.e., a CSS.

Model of fig. 1 panels D to F

The intrinsic growth rate $r(x)$ is given by a saturating function of the Michaelis–Menten form,

$$r(x) = r_m \cdot \frac{x}{h_r + x} \text{ with } x > 0. \tag{S1.12}$$

Parameters are r_m the maximum intrinsic growth rate and h_r the half saturation constant. Note that $r(x) > 0$ for all trait values $x > 0$. The fitness gradient equals

$$\left.\frac{\partial \omega(x_m, x)}{\partial x_m}\right|_{x_m=x} = \left.\frac{dr(x_m)}{dx_m}\right|_{x_m=x} = \frac{dr(x)}{dx} = r_m \cdot \frac{x}{(h_r + x)^2} > 0, \tag{S1.13}$$

which is always positive. Selection therefore always favours larger x phenotypes, so that evolution also maximizes intrinsic growth rates and abundances.

Mathematical detail for the second scenario

The invasion fitness of the second scenario reads as

$$\omega(x_m, x) = r(x_m) - \alpha(x_m) \cdot N^*(x). \tag{S1.14}$$

As a consequence, the fitness gradient is given by

$$\begin{aligned}\left.\frac{\partial\omega(x_m,x)}{\partial x_m}\right|_{x_m=x} &= \left.\frac{dr(x_m)}{dx_m}\right|_{x_m=x} - \left.\frac{d\alpha(x_m)}{dx_m}\right|_{x_m=x}\cdot N^*(x)\\ &= \frac{dr(x)}{dx} - \frac{d\alpha(x)}{dx}\cdot N^*(x).\end{aligned} \tag{S1.15}$$

This prove equation (6) of the main text. The abundance at ecological equilibrium equals $N^*(x) = r(x)/\alpha(x)$, consequently its derivative relative to x equals

$$\begin{aligned}\frac{dN^*(x)}{dx} &= \frac{1}{\alpha(x)}\cdot\frac{dr(x)}{dx} - \frac{r(x)}{(\alpha(x))^2}\cdot\frac{d\alpha(x)}{dx}\\ &= \frac{1}{\alpha(x)}\cdot\left(\frac{dr(x)}{dx} - \frac{d\alpha(x)}{dx}\cdot N^*(x)\right)\\ &= \frac{1}{\alpha(x)}\cdot\left.\frac{\partial\omega(x_m,x)}{\partial x_m}\right|_{x_m=x}\end{aligned} \tag{S1.16}$$

Within the bracket we can recognize the fitness gradient (equ. S1.2), which proves equation (7) of the main text. The second partial derivative of the invasion fitness is given by

$$\begin{aligned}\left.\frac{\partial^2\omega(x_m,x)}{\partial x_m^2}\right|_{x_m=x} &= \left.\frac{d^2r(x_m)}{dx_m^2}\right|_{x_m=x} - \left.\frac{d^2\alpha(x_m)}{dx_m^2}\right|_{x_m=x}\cdot N^*(x)\\ &= \frac{dr^2(x)}{dx^2} - \frac{d^2\alpha(x)}{dx^2}\cdot N^*(x).\end{aligned} \tag{S1.17}$$

To relate it to the second derivative of $N^*(x)$, it is easier to start from equation (S1.16) and to take the derivative of the second row

$$\begin{aligned}\frac{d^2N^*(x)}{dx^2} =& -\frac{1}{(\alpha(x))^2}\cdot\frac{d\alpha(x)}{dx}\cdot\left(\frac{dr(x)}{dx} - \frac{d\alpha(x)}{dx}\cdot N^*(x)\right)\\ &+ \frac{1}{\alpha(x)}\cdot\left(\frac{d^2r(x)}{dx^2} - \frac{d^2\alpha(x)}{d^2x}\cdot N^*(x)\right)\\ &- \frac{1}{\alpha(x)}\frac{d\alpha(x)}{dx}\cdot\frac{dN^*(x)}{dx}\end{aligned} \tag{S1.18}$$

On the first row, we recognize the fitness gradient, and on the second row the second derivative of the invasion fitness. Consequently, this equation also reads as

$$\begin{aligned}\frac{d^2N^*(x)}{dx^2} = & - \frac{1}{(\alpha(x))^2}\cdot\frac{d\alpha(x)}{dx}\cdot\left.\frac{\partial\omega(x_m,x)}{\partial x_m}\right|_{x_m=x} \\ & + \frac{1}{\alpha(x)}\cdot\left.\frac{\partial^2\omega(x_m,x)}{\partial x_m^2}\right|_{x_m=x} \\ & - \frac{1}{\alpha(x)}\frac{d\alpha(x)}{dx}\cdot\frac{dN^*(x)}{dx}\end{aligned} \tag{S1.19}$$

When evaluated at a singular strategy $\hat{x}$ it simplifies to

$$\left.\frac{d^2N^*(x)}{dx^2}\right|_{x=\hat{x}} = \frac{1}{\alpha(x)}\cdot\left.\frac{\partial^2\omega(x_m,x)}{\partial x_m^2}\right|_{x_m=x=\hat{x}}. \tag{S1.20}$$

This proves that an invasible strategy correspond to a local minimum in abundance, while a non-invasible strategy to a local maximum in abundance. The crossed derivative is simpler to compute and is given by

$$\left.\frac{\partial^2\omega(x_m,x)}{\partial x_m\partial x}\right|_{x_m=x} = \frac{d\alpha(x)}{dx}\cdot\frac{dN^*(x)}{dx}. \tag{S1.21}$$

As a singular strategy is also an optimum in $N*(x)$, the crossed derivative vanishes at a singular strategy. Therefore, singular strategies can only be either 1) convergent and non-invasible, i.e., CSS, or 2) non-convergent and invasible, i.e., repellor. Moreover, with the second partial derivative, we conclude that the singular strategy is non-invasible (and therefore a CSS) if and only if the intrinsic growth rate (or species abundance) is at a local maximum (negative second derivative). Similarly, the singular strategy is invasible (and therefore a repellor) if and only if and only if the intrinsic growth rate (or species abundance) is at a local minimum (positive second derivative).

Model of fig. 2 panels A to C

The intrinsic growth rate $r(x)$ and the intra-specific competition are functions are given by

$$r(x) = r_m\cdot\frac{x}{h_r+x} \quad \alpha x = \alpha_o x^\delta \text{ with } x > 0 \tag{S1.22}$$

Parameters are r_m the maximum intrinsic growth rate and h_r the half-saturation, and $0 < \delta < 1$ determines the shape of the trade-off function and α_o its amplitude. Note that $r(x) > 0$ for all trait value $x > 0$. The relative fitness function of a rare mutant x_m in a resident population x is given by

$$\omega(x_m, x) = r(x_m) - \alpha(x_m) \cdot N^*(x) = r_m \cdot \left(\frac{x_m}{h_r + x_m} - \frac{x_m^{\delta} \cdot x^{1-\delta}}{h_r + x} \right). \tag{S1.23}$$

Then, the fitness gradient equals

$$\begin{aligned} \left. \frac{\partial \omega(x_m, x)}{\partial x_m} \right|_{x_m = x} &= \frac{dr(x)}{dx} - \frac{d\alpha(x)}{dx} \cdot N^*(x) \\ &= r_m \cdot \left(\frac{h_r}{(h_r + x)^2} - \frac{\delta}{h_r + x} \right). \end{aligned} \tag{S1.24}$$

It equals zero at $x^* = h \cdot (1 - \delta)/\delta$.

Model of fig. 2 panels D to F

The intrinsic growth rate $r(x)$ and the intra-specific competition are given by

$$r(x) = r_m \cdot e^{-\lambda_r x} \quad \alpha x = \alpha_m \cdot e^{-\lambda_\alpha x} \text{ with } x > 0 \tag{S1.25}$$

Parameters are r_m the maximum intrinsic growth rate, α_m the maximum level of intra-specific competition, $\lambda_r > 0$ the rate at which the intrinsic growth rate decreases with the trait value x, and $\lambda_\alpha > 0$ the rate at which the intrinsic growth rate decreases with the trait value x. Note that $r(x) > 0$ for all trait value $x > 0$. Thus, the ecological equilibrium is given by

$$N^*(x) = \frac{r(x)}{\alpha(x)} = \frac{r_m}{\alpha_m} \cdot e^{-(\lambda_r - \lambda_\alpha) \cdot x} \tag{S1.26}$$

The relative fitness function of a rare mutant x_m in a resident population x is given by

$$\omega(x_m, x) = r(x_m) - \alpha(x_m) \cdot N^*(x) = r_m \cdot \left(e^{-\lambda_r x_m} - \cdot e^{-\lambda_\alpha x_m} \cdot e^{-(\lambda_r - \lambda_\alpha) \cdot x} \right). \tag{S1.27}$$

The fitness gradient equals

$$\begin{aligned} \left. \frac{\partial \omega(x_m, x)}{\partial x_m} \right|_{x_m = x} &= \frac{dr(x)}{dx} - \frac{d\alpha(x)}{dx} \cdot N^*(x) \\ &= r_m \cdot e^{-\lambda_r x} \cdot (\lambda_\alpha - \lambda_r). \end{aligned} \tag{S1.28}$$

Note that the signe of the evolutive gradient is given by the sign of $\lambda_\alpha - \lambda_r$. Thus, phenotypic traits converge either to $x^* = 0$ if $\lambda_\alpha - \lambda_r < 0$ or to $x^* \to \infty$ if $\lambda_\alpha - \lambda_r > 0$. In both cases, evolution selectes phentoypes with larger abundance, as function of equation

(S1.26) decreases if $\lambda_\alpha - \lambda_r < 0$ and increases if $\lambda_\alpha - \lambda_r > 0$.

Mathematical detail for the third scenario

The invasion fitness of the third scenario reads as

$$\omega(x_m, x) = r(x_m) - \alpha(x_m, x) \cdot N^*(x). \tag{S1.29}$$

As a consequence, the fitness gradient is given by

$$\begin{aligned} \left.\frac{\partial \omega(x_m, x)}{\partial x_m}\right|_{x_m=x} &= \left.\frac{dr(x_m)}{dx_m}\right|_{x_m=x} - \left.\frac{\partial \alpha(x_m, x)}{\partial x_m}\right|_{x_m=x} \cdot N^*(x) \\ &= \frac{dr(x)}{dx} - \left.\frac{\partial \alpha(x_m, x)}{\partial x_m}\right|_{x_m=x} \cdot N^*(x). \end{aligned} \tag{S1.30}$$

This prove equation (9) of the main text. The abundance at ecological equilibrium equals $N^*(x) = r(x)/\alpha(x, x)$, consequently its derivative relative to x equals

$$\begin{aligned} \frac{dN^*(x)}{dx} =& \frac{1}{\alpha(x,x)} \cdot \frac{dr(x)}{dx} - \frac{r(x)}{(\alpha(x,x))^2} \cdot \left.\frac{\partial \alpha(x', x)}{\partial x'}\right|_{x'=x} - \frac{r(x)}{(\alpha(x,x))^2} \cdot \left.\frac{\partial \alpha(x, x')}{\partial x'}\right|_{x'=x} \\ =& \frac{1}{\alpha(x,x)} \cdot \left(\frac{dr(x)}{dx} - \left.\frac{\partial \alpha(x', x)}{\partial x'}\right|_{x'=x} \cdot N^*(x) - \left.\frac{\partial \alpha(x, x')}{\partial x'}\right|_{x'=x} \cdot N^*(x) \right) \\ =& \frac{1}{\alpha(x,x)} \cdot \left(\left.\frac{\partial \omega(x_m, x)}{\partial x_m}\right|_{x_m=x} - \left.\frac{\partial \alpha(x, x')}{\partial x'}\right|_{x'=x} \cdot N^*(x) \right). \end{aligned} \tag{S1.31}$$

In the first two terms in the second row bracket, we can recognize the evolutive gradient. Thus, this expression can be rewritten as

$$\frac{dN^*(x)}{dx} = \frac{1}{\alpha(x,x)} \cdot \left(\left.\frac{\partial \omega(x_m, x)}{\partial x_m}\right|_{x_m=x} - \left.\frac{\partial \alpha(x_m, x)}{\partial x}\right|_{x_m=x} \cdot N^*(x) \right). \tag{S1.32}$$

This proves equation (10) of the main text. As already explained in the main text, equations (S1.30 and S1.31) imply that a singular strategy do not correspond to local optimum in abundance or in intrinsic growth rate (unless we are in a particular case; as explained in the main text). The crossed derivative is given by

$$\left.\frac{\partial^2 \omega(x_m, x)}{\partial x_m \partial x}\right|_{x_m=x} = \left.\frac{d\alpha(x_m, x)}{dx_m}\right|_{x_m=x} \cdot \frac{dN^*(x)}{dx}. \tag{S1.33}$$

As a singular strategy is not an optimum in $N^*(x)$, the crossed derivative does not vanish at a singular strategy. Therefore, any types of singular strategy are possible.

S2: Details for the two co-evolving morphs

The ecological dynamics of two morphs of traits x_1 and x_2 is given by the classical Lotka-Volterra model of competition. The intrinsic growth rate $r(x_i)$ and interaction strength $\alpha(x_i, x_j)$ are functions of the phenotypes traits x_1 and x_2 and the Lotka-Volterra model is given by:

$$\begin{cases} \dfrac{dN_1}{dt} = N_1 \cdot (r(x_1) - \alpha(x_1, x_1) \cdot N_1 - \alpha(x_1, x_2) \cdot N_2) \\ \dfrac{dN_2}{dt} = N_2 \cdot (r(x_2) - \alpha(x_2, x_1) \cdot N_2 - \alpha(x_2, x_2) \cdot N_2) \end{cases} \tag{S2.1}$$

The niche-overlap ρ and fitness-difference κ metrics *sensu* coexistence theory are given by

$$\rho = \sqrt{\frac{\alpha(x_1, x_2)\alpha(x_2, x_1)}{\alpha(x_1, x_1)\alpha(x_2, x_2)}} \qquad \text{and} \qquad \kappa = \frac{r(x_1)}{r(x_2)} \cdot \sqrt{\frac{\alpha(x_2, x_2)\alpha(x_2, x_1)}{\alpha(x_1, x_1)\alpha(x_1, x_2)}}, \tag{S2.2}$$

and coexistence between the two morphs is reached if and only if

$$\frac{1}{\rho} > \kappa > \rho. \tag{S2.3}$$

S3: Mathematical proof of the gradient-based approach – monomorphic case

In this appendix, we give the full mathematical proof of our results. We will start by showing that class I models lead to evolution that optimizes (local maximum or minimum) the property P^* and to evolutionary singular strategies that can only be CSS or reppelor. Then we will explain why for class II models, such optimization principles do not generally hold, and why any type of singular strategies can be expected.

Class I of relative fitness function; optimization

The proof works as follows. First, let us assume that the system is at its ecological equilibrium. By definition of such an ecological equilibrium, the following equality must be fulfilled:

$$f(x, P^*(x)) = 0. \tag{S3.1}$$

This is so, because $f^I(x, P^*(x))$ is the *per capita* growth of a resident phenotype in a resident population at is ecological equilibrium. By taking the derivative relative to x on both side we obtain,

$$\left.\frac{\partial f^I(x_1, P^*(x))}{\partial x_1}\right|_{x_1=x} + \left.\frac{\partial f^I(x, P)}{\partial P}\right|_{P=P^*(x)} \cdot \frac{dP^*(x)}{dx} = 0. \tag{S3.2}$$

The fitness gradient is by definition

$$\left.\frac{\partial \omega(x_m, x)}{\partial x_m}\right|_{x_m=x} = \left.\frac{\partial f^I(x_m, P^*(x))}{\partial x_m}\right|_{x_m=x}. \tag{S3.3}$$

Combining these two equations results in

$$\left.\frac{\partial \omega(x_m, x)}{\partial x_m}\right|_{x_m=x} = -\left.\frac{\partial f^I(x, P)}{\partial P}\right|_{P=P^*(x)} \cdot \frac{dP^*(x)}{dx}, \tag{S3.4}$$

which is equation (21) of the main text.

The cross derivative is given by

$$\left.\frac{\partial^2 \omega(x_m, x)}{\partial x \partial x_m}\right|_{x_m=x} = \left.\frac{\partial^2 f^I(x_m, P)}{\partial P \partial x_m}\right|_{x_m=x, P=P^*(x)} \cdot \frac{dP^*(x)}{dx}. \tag{S3.5}$$

As an evolutionary singular strategy x^* corresponds to a local maximum or minimum in

P^*, the cross derivative vanishes at x^*. This proves that x^* can only be a CSS (convergent and non invasible) or a repellor (non-convergent and invasible), depending on the sign of the second derivative of the relative fitness function. A positive second derivative corresponds to a CSS, while a negative value results in a repellor.

Finally, we relate the second derivative of the relative fitness function to the second derivative of the property P^*. To do so, we take the second derivative, relative to the evolving traits x, of the equilibrium condition, $f^I(x, P(x)) = 0$. It leads to

$$\begin{aligned} &\left.\frac{\partial^2 f^I(x,P)}{\partial x^2}\right|_{P=P^*(x)} + 2 \cdot \left.\frac{\partial f(x,P)}{\partial P \partial x}\right|_{P=P^*(x)} \cdot \frac{dP^*(x)}{dx} \\ &+ \left.\frac{\partial^2 f^I(x,P)}{\partial P^2}\right|_{P=P^*(x)} \cdot \left(\frac{dP^*(x)}{dx}\right)^2 + \left.\frac{\partial f^I(x,P)}{\partial P}\right|_{P=P^*(x)} \cdot \frac{d^2 P^*(x)}{dx^2} = 0. \end{aligned} \tag{S3.6}$$

At an evolutionary singular point x^* the first derivative of $P^*(x)$ vanishes. Moreover, the first term equals the second derivative of the relative fitness function. Therefore, we obtain the following equivalence,

$$\left.\frac{\partial^2 \omega(x_m, x)}{\partial x_m^2}\right|_{x_m=x=x^*} = - \left.\frac{\partial f^I(x^*, P)}{\partial P}\right|_{P=P^*(x^*)} \cdot \frac{d^2 P^*(x^*)}{(dx^*)^2}. \tag{S3.7}$$

Depending on the sign of $\partial f(x,P)/\partial N|_{P=P^*(x)}$, the second derivative of the relative fitness function has the same, or opposite, sign as the second derivative of P^*.

Class II fitness functions; non-optimisation

We now show that for class II models, such an optimization principle does not hold. Again, at the ecological equilibrium we have,

$$f^{II}(x, x, P^*(x)) = 0. \tag{S3.8}$$

By taking its derivative relative to x, we obtain

$$\begin{aligned} &\left.\frac{\partial f^{II}(x_1, x, P^*(x))}{\partial x_1}\right|_{x_1=x} + \left.\frac{\partial f^{II}(x, x_2, P^*(x))}{\partial x_2}\right|_{x_2=x} \\ &\qquad + \left.\frac{\partial f^{II}(x,x,P)}{\partial P}\right|_{P=P^*(x)} \cdot \frac{dP^*(x)}{dx} = 0. \end{aligned} \tag{S3.9}$$

In the first term we can recognize the fitness gradient. Consequently we obtain

$$\begin{aligned} \left.\frac{\partial \omega(x_m, x)}{\partial x_m}\right|_{x_m=x} = & -\left.\frac{\partial f^{II}(x, x, P)}{\partial P}\right|_{P=P^*(x)} \cdot \frac{dP^*(x)}{dx} \\ & -\left.\frac{\partial f^{II}(x, x_2, P^*(x))}{\partial x_2}\right|_{x_2=x}, \end{aligned} \tag{S3.10}$$

which is equation (22) of the main text. The term $\partial f^{II}(x, x_2, P^*(x))/\partial x_2|_{x_2=x}$ does not necessarily equal zero, so that an evolutionary singularity is no longer equivalent to a local optimum in P^*.

Moreover, the cross derivative of the relative fitness function, in class II, equals to

$$\begin{aligned} \left.\frac{\partial^2 \omega(x_m, x)}{\partial x \partial x_m}\right|_{x_m=x} = & \left.\frac{\partial^2 f(x_m, x, P)}{\partial P \partial x_m}\right|_{x_m=x, P=P^*(x)} \cdot \frac{dP^*(x)}{dx} \\ & + \left.\frac{\partial^2 f(x_m, x, P)}{\partial x \partial x_m}\right|_{x_m=x, P=P^*(x)}, \end{aligned} \tag{S3.11}$$

which, in general, does not vanish. This shows that, in general, evolution in class II models does not optimize P^*, and that any type of evolutionary singular strategy is possible.

S4: Example with multiplicative separable competition function

In this appendix, we detailed the example with a multiplicative separable competition function. That is, we assume that the competition strength of a resident phenotype x on a mutant x_m as the form

$$\alpha(x_m, x) = c(x_m)\sigma(x). \tag{S4.1}$$

The abundance at ecological equilibrium is given by

$$N^*(x) = \frac{r(x)}{c(x)\sigma(x)}, \tag{S4.2}$$

and the invasion fitness by

$$\omega(x_m, x) = r(x_m) - c(x_m)\sigma(x)N^*(x). \tag{S4.3}$$

By replacing the equilibrium abundance into this expression, we obtain

$$\omega(x_m, x) = r(x_m) - c(x_m)\sigma(x)\frac{r(x)}{c(x)\sigma(x)} = r(x_m) - c(x_m)\frac{r(x)}{c(x)}. \tag{S4.4}$$

This expression can be rewritten into the four equivalent forms:

$$\begin{aligned}\omega(x_m, x) =& c(x_m)\left(\frac{r(x_m)}{c(x_m)} - \frac{r(x)}{c(x)}\right)\\ =& c(x_m)\left(\sigma(x_m)N^*(x_m) - \sigma(x)N^*(x)\right)\\ =& r(x_m) - \frac{c(x_m)}{c(x)}r(x)\\ =& c(x_m)\sigma(x_m)\left(N^*(x_m) - \frac{\sigma(x)}{\sigma(x_m)}N^*(x)\right)\end{aligned} \tag{S4.5}$$

The first two rows Imply that the invasion fitness is of class I for the property $P^*(x) = \frac{r(x)}{c(x)} = \sigma(x_m)N^*(x_m)$. That is, evolution optimizes this quantity, and branching is not allowed. The last two rows imply that evolution does not optimize r neither N^*. But as evolution optimizes $\frac{r(x)}{c(x)} = \sigma(x_m)N^*(x_m)$ branching is not allowed and evolution converges to a CSS.

We reach the exact same conclusion by applying coexistence theory. The niche overlap is given by

$$\rho = \sqrt{\frac{c(x_m)\sigma(x)c(x)\sigma(x_m)}{c(x)\sigma(x)c(x_m)\sigma(x_m)}} = 1, \tag{S4.6}$$

which indicates that branching is impossible and that the selected phenotypes is determined by the fitness ratio,

$$\kappa = \frac{r(x)}{r(x_m)}\sqrt{\frac{c(x_m)\sigma(x_m)c(x_m)\sigma(x)}{c(x)\sigma(x)c(x)\sigma(x)}} = \frac{r(x)/c(x)}{r(x_m)/c(x_m)} = \frac{\sigma(x)N^*(x)}{\sigma(x_m)N^*(x_m)}. \tag{S4.7}$$

Thus we reach the same conclusion that evolution selects phenotype with larger $\frac{r(x)}{c(x)} = \sigma(x)N^*(x)$.

In conclusion, this invasion fitness is of class I when one consider the property $\frac{r(x)}{c(x)} = \sigma(x)N^*(x)$, but of class II when one consider the property r or N^*.

S5: Mathematical proof of the gradient-based approach – polymorphic case

In this appendix, we extend the proofs in Supporting Material S3 to the polymorphic case.

Class I of relative fitness function; optimization

Let us assume that the system is at ecological equilibrium at which the following set of equations hold:

$$\begin{cases} f_1^I(x_1, \boldsymbol{P}^*(\boldsymbol{x})) = 0 \\ \vdots \\ f_n^I(x_n, \boldsymbol{P}^*(\boldsymbol{x})) = 0 \end{cases} \tag{S5.1}$$

The relative fitness function of, and its derivative for a mutant $x_{i,m}$ of phenotype i are given by

$$\omega_i(x_{i,m}, \boldsymbol{x}) = f_i^I(x_{i,m}, \boldsymbol{P}^*(\boldsymbol{x})) \quad \text{and} \quad \left.\frac{\partial \omega_i(x_{i,m}, \boldsymbol{x})}{\partial x_{i,m}}\right|_{x_{i,m}=x_i} = \frac{\partial f_i^I(x_i, \boldsymbol{P}^*(\boldsymbol{x}))}{\partial x_i} \tag{S5.2}$$

As in the monomorphic case, we can relate the fitness gradient to the property $\boldsymbol{P}^*$ derivative in the following way. We take the derivative of the set of equilibrium equations (S5.1) relative to the traits x_i of phenotypes i. This results in the following set of linear equation for the property partial derivative $\partial \boldsymbol{P}^*/\partial x_i$:

$$\begin{cases} \dfrac{\partial f_1^I(x_1, \boldsymbol{P}^*(\boldsymbol{x}))}{\partial x_i} = -\dfrac{\partial f_1^I(x_1, \boldsymbol{P}^*(\boldsymbol{x}))}{\partial P_1} \cdot \dfrac{\partial P_1}{\partial x_i} \cdots - \dfrac{\partial f_1^I(x_1, \boldsymbol{P}^*(\boldsymbol{x}))}{\partial P_n} \cdot \dfrac{\partial P_n}{\partial x_i} \\ \vdots \\ \dfrac{\partial f_n^I(x_n, \boldsymbol{P}^*(\boldsymbol{x}))}{\partial x_i} = -\dfrac{\partial f_n^I(x_n, \boldsymbol{P}^*(\boldsymbol{x}))}{\partial P_1} \cdot \dfrac{\partial P_1}{\partial x_i} \cdots - \dfrac{\partial f_n^I(x_n, \boldsymbol{P}^*(\boldsymbol{x}))}{\partial P_n} \cdot \dfrac{\partial P_n}{\partial x_i} \end{cases} \tag{S5.3}$$

This set of linear equation can be rewritten in a matrix format as

$$\begin{bmatrix} \frac{\partial f_1^I(x_1, \boldsymbol{P}^*(\boldsymbol{x}))}{\partial x_i} \\ \vdots \\ \frac{\partial f_n^I(x_n, \boldsymbol{P}^*(\boldsymbol{x}))}{\partial x_i} \end{bmatrix} = -\boldsymbol{\alpha} \cdot \frac{\partial \boldsymbol{P}^*(\boldsymbol{x})}{\partial x_i}. \tag{S5.4}$$

The elements of the matrix $\boldsymbol{\alpha}$ are the partial derivatives $\partial f_i^I(x_i, \boldsymbol{P}^*(\boldsymbol{x}))/\partial P_j$ of the per capita growth rate relative to the property $\boldsymbol{P}^*$. For class I fitness functions, all terms of the vector of the left term equals zero except for the element i:

$$\begin{bmatrix} \frac{\partial f_1^I(x_1,\boldsymbol{P}^*(\boldsymbol{x}))}{\partial x_i} \\ \vdots \\ \frac{\partial f_n^I(x_n,\boldsymbol{P}^*(\boldsymbol{x}))}{\partial x_i} \end{bmatrix} = \begin{bmatrix} 0 \\ \left.\frac{\partial \omega_i(x_{i,m},\boldsymbol{x})}{\partial x_{i,m}}\right|_{x_{i,m}=x_i} \\ 0 \end{bmatrix}. \tag{S5.5}$$

This results in the following equivalence between the fitness gradient and the property $\boldsymbol{P}^*$:

$$\begin{bmatrix} 0 \\ \left.\frac{\partial \omega_i(x_{i,m},\boldsymbol{x})}{\partial x_{i,m}}\right|_{x_{i,m}=x_i} \\ 0 \end{bmatrix} = -\boldsymbol{\alpha} \cdot \frac{\partial \boldsymbol{N}^*(\boldsymbol{x})}{\partial x_i}. \tag{S5.6}$$

This equation is the generalization to polymorphic (or species) coevolution of the equation (21) of the monomorphic case. This equation shows the equivalence between properties optimum and singular strategies.

Following the same line as in the monomorphic demonstration, we compute the cross derivative of the relative fitness for each phenotype i,

$$\left.\frac{\partial^2 \omega_i(x_{i,m},\boldsymbol{x})}{\partial x_j \partial x_{i,m}}\right|_{x_{i,m}=x_i} = \sum_{k=1}^{n} \left.\frac{\partial^2 f_i^I(x_{i,m},\boldsymbol{P})}{\partial P_k \partial x_{i,m}}\right|_{x_{i,m}=x_i,\boldsymbol{P}=\boldsymbol{P}^*(\boldsymbol{x})} \cdot \frac{\partial P_k^*(\boldsymbol{x})}{\partial x_j}. \tag{S5.7}$$

As the partial derivatives of the property $\boldsymbol{P}^*$ vanishes at singular strategies, the cross derivatives also equal zeros at singular strategies. This demonstrates that a singular strategy can either be convergent and evolutionary stable (CSS), or non-convergent and evolutionary non-stable (repellor).

Finally, the second derivative relation (equation S3.7 in the monomorphic case) generalizes to the polymorphic case as

$$\begin{bmatrix} 0 \\ \left.\frac{\partial^2 \omega_i(x_{i,m},\boldsymbol{x})}{\partial x_{i,m}^2}\right|_{x_{i,m}=x_i} \\ 0 \end{bmatrix} = -\boldsymbol{\alpha} \cdot \frac{\partial^2 \boldsymbol{P}^*(\boldsymbol{x})}{\partial x_i^2}. \tag{S5.8}$$

This equation generalizes (equ. S3.7) of the monomorphic case.

Class II fitness functions; non-optimisation

The main difference with the class I of relative function is that in the vector

$$\begin{bmatrix} \frac{\partial f_1^{II}(x_1,\boldsymbol{x},\boldsymbol{P}^*(\boldsymbol{x}))}{\partial x_i} \\ \vdots \\ \frac{\partial f_n^{II}(x_n,\boldsymbol{x},\boldsymbol{P}^*(\boldsymbol{x}))}{\partial x_i} \end{bmatrix} \tag{S5.9}$$

none of the terms

$$\frac{\partial f_j^{II}(x_j,\boldsymbol{x},\boldsymbol{P}^*(\boldsymbol{x}))}{\partial x_i} \quad \text{for} \quad i \neq j \tag{S5.10}$$

vanish in general. This is so, because of the presence of the term $\boldsymbol{x}$ in the relative fitness function. That is, in general,

$$\begin{bmatrix} \frac{\partial f_1^{II}(x_1,\boldsymbol{x},\boldsymbol{P}^*(\boldsymbol{x}))}{\partial x_i} \\ \vdots \\ \frac{\partial f_n^{II}(x_n,\boldsymbol{x},\boldsymbol{P}^*(\boldsymbol{x}))}{\partial x_i} \end{bmatrix} \neq \begin{bmatrix} 0 \\ \left.\frac{\partial \omega_i(x_{i,m},\boldsymbol{x})}{\partial x_{i,m}}\right|_{x_{i,m}=x_i} \\ 0 \end{bmatrix}, \tag{S5.11}$$

consequently, coevolution does not lead to abundance optimization and any type of singular strategies is possible.