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The Evolution of Resource Specialization Through Frequency-Dependent and Frequency-Independent Mechanisms

Claus Rueffler (rueffler@zoo.utoronto.ca)
Tom J.M. Van Dooren (vdooren@rulsfb.leidenuniv.nl)
Johan A.J. Metz (j.a.j.metz@biology.leidenuniv.nl)

Approved by

Ulf Dieckmann
Program Leader, Evolution and Ecology Program

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Contents

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Claus Rueffler[1], Tom J.M. Van Dooren[2], and Johan A. J. Metz[3,4]

Institute of Biology Leiden, Leiden University, Kaiserstraat 63, 2311 GP Leiden
The Netherlands

ABSTRACT

Levins' fitness set approach has shaped the intuition of many evolutionary ecologists about resource specialization: if the set of possible phenotypes is convex, a generalist is favored, while either of the two specialists is predicted for concave phenotype sets. An important aspect of Levins' approach is that it explicitly excludes frequency-dependent selection. Frequency-dependence emerged in a series of models that studied the degree of character displacement of two consumers coexisting on two resources. Surprisingly, the evolutionary dynamics of a single consumer type under frequency-dependence has not been studied in detail yet. We analyze a model of one evolving consumer feeding on two resources and show that, depending on the trait considered to be subject to evolutionary change, selection is either frequency-independent or frequency-dependent. This difference is explained by the effects different foraging traits have on the consumer-resource interactions. If selection is frequency-dependent, then the population can become dimorphic through evolutionary branching at the trait value of the generalist. Those traits with frequency-independent selection, however, do indeed follow the predictions based on Levins' fitness set approach. This dichotomy in the evolutionary dynamics of traits involved in the same foraging process was not previously recognized.

Subject headings: evolutionary branching, frequency-dependent selection, generalist, specialist, trade-off

1. Introduction

In the presence of different resources, when should we expect a generalist phenotype and when specialized phenotypes? This question has a long history in evolutionary ecology (for reviews see

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[1]corresponding author, present address: Department of Zoology, University of Toronto 25 Harbord St., Toronto, Ontario, M5S 3G5, Canada, rueffler@zoo.utoronto.ca

[2]vdooren@rulsfb.leidenuniv.nl

[3]metz@rulsfb.leidenuniv.nl

[4]Adaptive Dynamics Network, International Institute of Applied Systems Analysis, A-2361 Laxenburg, Austria

Futuyma and Moreno (1988); Wilson and Yoshimura (1994)). One of the first answers to this question, which is still widely accepted, was given by Levins (1962) and is based on the shape of the fitness set, i.e., on the set of feasible phenotypes. A consumer feeding on two different resources should be equally well adapted to both of them, when the fitness set is convex (corresponding to a weak trade-off). In this case the fitness of a consumer summed over the two resources is higher for a generalist than for either to the two specialists. On the other hand, in case of a concave fitness set (corresponding to a strong trade-off) both specialists do better than a generalist and a consumer population is expected to specialize on either of the two resources.

A serious shortcoming of Levins approach is that it explicitly excludes the possibility of density-dependent and frequency-dependent selection. These features cause the fitness corresponding to a particular trait value to depend on that trait value as well as on the frequency and abundance of other trait values in the population. In this case the fitness landscape is not fixed anymore but changes with population composition (Rueffler et al. 2004). Density- and frequency-dependence arise in a natural way when resource consumption and renewal are modeled explicitly. In this context, frequency-dependence has to be understood in a generalized sense. It can arise from direct interactions between different phenotypes, but it can also be mediated by variables like resource densities that depend on the composition of the consumer population.

MacArthur and Levins (1964) were the first to introduce a model for the coevolution of two consumers feeding on two resources with explicit dynamics. Their model was analyzed by Lawlor and Maynard Smith (1976) using an ESS approach (Maynard Smith 1982), subsequently put into a population genetics framework by Lundberg and Stenseth (1985), and extended to more traits by Abrams (1986). The evolution of a single consumer was treated incompletely by these authors, maybe because it was considered trivial according to the predictions of Levins' earlier treatment. That this is far from true became apparent from a paper of Wilson and Turelli (1986). They used a similar setting to explore the conditions under which a population of homozygotes, specialized on one resource, can be invaded by a new allele that causes the heterozygote to be a generalist and the mutant homozygote to be more specialized for another resource. The unexpected result of Wilson and Turelli is that such an invasion is possible even with marginal underdominance, i.e., when the efficiency of the heterozygote summed over the two resources is lower than the same sum for each of the two homozygotes. For a single diallelic locus marginal underdominance is equivalent to a strong trade-off (Lundberg and Stenseth 1985; Wilson and Turelli 1986). Levins' approach therefore would predict evolution towards specialization. However, invasion of the heterozygote can be seen as evolution in the direction of the generalist. For a wide range of parameters the new allele does not go to fixation but coexists in a stable polymorphism. The result of Wilson and Turelli is of particular importance, because at population genetical equilibrium the heterozygote has the lowest fitness and any mechanism preventing the production of the heterozygote is selected for. Such convergence stable fitness minima were named evolutionary branching points by Metz et al. (1996a) and Geritz et al. (1998).

Wilson and Turelli (1986) investigate the dynamics of mutations with large phenotypic effect.

A mutant arising from a specialist for one resource immediately is a specialist for another resource and both types can therefore coexist in a protected dimorphism. Is it also possible to obtain two specialists by accumulation of mutations with small effects? In this paper we analyze the evolution of a single consumer foraging on two resources with explicit dynamics. Instead of formulating a population genetics model we assume clonal reproduction with rare mutations. This allows us to use the toolbox of adaptive dynamics (Metz et al. 1992, 1996a; Geritz et al. 1998; Diekmann 2004). The assumption of clonal reproduction may seem a limitation. However, in the limit of rare mutations with small phenotypic effect and random mating, the results carry over to monomorphic diploid populations and polygenic traits (Van Dooren in press; Metz in press). Additionally, this approach yields the same results as models derived from quantitative genetics (Iwasa et al. 1991; Taper and Case 1992; Abrams et al. 1993a).

Lawlor and Maynard Smith (1976) and Wilson and Turelli (1986) assume a linear (type I) functional response. In our model we assume that handling time is an important component of the foraging process and that therefore the resource uptake is governed by a saturating (type II) functional response. Due to this assumption our model involves more traits than those considered by earlier authors (but see Abrams (1986)) and the question arises whether different traits involved in the foraging process differ in their evolutionary dynamics. A major goal of our paper is therefore to compare the evolutionary dynamics of different traits.

We find that the evolutionary dynamics of different traits fall into two different categories. In one category the dynamics are driven by frequency-dependent selection while in the other case selection is frequency-independent. For traits under frequency-dependent selection the trait value of the generalist is approached for both weak and strong trade-offs. In the first case it is the end point of evolution while in the latter case it is a branching point where protected polymorphisms can emerge by small mutational steps. For traits experiencing frequency-independent selection the classical predictions of Levins apply, though we can not use his methodology in general. For such traits two different consumers can generically not coexist.

2. The Model

In this section we develop a population dynamical model for a consumer feeding on two nutritionally substitutable resources which are assumed to be homogeneously distributed in space. From this model, we will derive invasion fitness which we use to investigate the evolutionary dynamics. Table 1 gives an overview of all model parameters.

2.1. Population Dynamics

The population dynamics of the consumer and the two resources are similar to those described by Wilson and Turelli (1986). The consumer is an annual organism with its population census after

juvenile mortality. Consumer densities are assumed to be constant within the foraging season. The dynamics of the resources occurs on a much faster time scale and are followed in continuous time within a year. Since the consumer density does not change on this time scale, resource densities reach an within-year equilibrium. We will first introduce the dynamics of the consumer as a function of the equilibrium densities of the resources reached within a year. In a second step we will derive the resource dynamics within a year and their equilibrium (c.f. Geritz and Kisdi 2004).

The recurrence equation for the consumer is given by

$$N_{t+1} = (\alpha_1 C_1 + \alpha_2 C_2) N_t, \tag{1}$$

where the functional response C_i describes the amount of resource of type i consumed as a function of resource density. The constant α_i is the conversion efficiency of consumed resource into offspring. Thus, a linear numerical response is assumed. Prey consumption is modeled by means of a two-species version of Holling's disk equation, which gives rise to a saturating (type II) functional response C_i for each resource i (Holling 1959):

$$C_i = \frac{e_i \hat{R}_{it} p_i f_i}{1 + e_1 \hat{R}_{1t} p_1 (t_{p1} + f_1 t_{m1}) + e_2 \hat{R}_{2t} p_2 (t_{p2} + f_2 t_{m2})} \qquad \text{for} \qquad i \in \{1, 2\}. \tag{2}$$

We use a rather detailed version of Holling's equation as described in Case (2000). In many biological systems not all elements will be of importance. Such a detailed model can be adapted by simplification to systems where only a subset of parameters is relevant. The number of encountered prey per time step is the product of search efficiency e_i [area/time step] and equilibrium resource density $\hat{R}_{it}$ [1/area] in a given year t. This introduces a time dependence into the functional responses, but we suppress the time index for clarity. The search efficiency e_i depends on the speed of the consumer while searching for prey, its search area and its ability to detect a prey item within the search area. Upon encounter the consumer decides to attack the prey with probability p_i. Throughout this paper we will assume that consumers behave opportunistically. Encountered prey is always attacked and therefore $p_1 = 1 = p_2$. Hence, we will omit the p's from now on. In a follow-up paper we will incorporate flexible diet choice. The capture probability f_i describes the probability that an attacked prey is actually subdued. The handling time consists of two components: the pursuit time t_{pi} and the manipulation time t_{mi}. The pursuit time is the time needed to get hold of a prey once it is detected. Caught prey might still need a treatment before it can be consumed, the duration of this treatment is the manipulation time. Note that the denominators of C_1 and C_2 are identical and can be factored out. This factor, to be called search probability,

$$s = 1 / \left(1 + e_1 \hat{R}_{1t}(t_{p1} + f_1 t_{m1}) + e_2 \hat{R}_{2t}(t_{p2} + f_2 t_{m2})\right) \tag{3}$$

is the fraction of a time step that is not spend handling prey but left for searching prey. We can therefore write Eq. (1) as

$$N_{t+1} = s \left(\alpha_1 e_1 \hat{R}_1 f_1 + \alpha_2 e_2 \hat{R}_2 f_2\right) N_t. \tag{4}$$

If both the pursuit and the handling time are negligible, then $s = 1$ and Eq. (4) describes the consumer's population dynamics according to a linear (type I) functional response. If only the pursuit time is negligible, the rather complicated formulas for the functional response and search probability simplify to the more familiar formulas $C_i = (e_i \hat{R}_{it})/(1 + e_1 \hat{R}_{1t} t_{m1} + e_2 \hat{R}_{2t} t_{m2})$ and $s = 1/(1 + e_1 \hat{R}_{1t} t_{m1} + e_2 \hat{R}_{2t} t_{m2})$ (e.g. Abrams 1986, 1987; there f_i is incorporated into e_i).

The within-year dynamics of the resources are given by

$$\frac{\mathrm{d}R_{it}}{\mathrm{d}\tau} = b_i - d_i R_{it} - C_i N_t \qquad \text{for} \qquad i \in \{1, 2\}, \tag{5}$$

where τ denotes time within a foraging season. We assume that the production of the resources is independent of their abundance. This might be the case when prey population size is more determined by migration (e.g., prey that is leaving a refuge at a constant rate), or for seeds or fruits produced by trees. The parameter b_i denotes the constant influx of resources and d_i its death rate. Since we assume consumer densities N_t to be constant within the foraging season, we can give the following implicit description of $\hat{R}_{it}$, the resource equilibria reached in year t, using Eq. (2) and (3):

$$\hat{R}_{it} = \frac{b_i}{d_i + s e_i f_i N_t} \qquad \text{for} \qquad i \in \{1, 2\}. \tag{6}$$

In order to calculate the equilibria of the consumer and resource dynamics across years, we have to solve Eq. (1) and (5) simultaneously using Eq. (2). The lengthy analytical expressions are not show here.

2.2. Trade-Offs

When a consumer feeds on two resources, trade-offs will occur almost inevitably. We will refer to the boundary of the set of feasible phenotypes as the trade-off curve (see Fig. 1). Beyond the trade-off curve either no genetic variation occurs or no viable offspring can be produced. Mutations that lead to an increase in efficiency for both resources are certainly favored by selection and cause the population's distribution of trait values to shift closer to the trade-off curve. Once the trade-off curve is reached, a mutation enhancing the consumer's efficiency for resource one will decrease its efficiency for resource two. From then on the population's distribution of trait values will stay close to the trade-off curve relative to the size of the mutational steps. We idealize this with the assumption that, after approaching it, the evolutionary dynamics proceeds along the trade-off curve. We define the trade-off curve as a function $x_2(x_1)$ in the (x_1, x_2)-space where x represents any of the traits we consider evolvable (Tab. 2). To simplify the analysis we parameterize the trade-off curve in one parameter θ, called specialization coefficient, which varies continuously between zero and one. Each θ determines a pair of trait values $\boldsymbol{x} = (x_1, x_2)$ lying on the trade-off curve in such a way that $\theta = 0$ corresponds to a specialist for resource one while $\theta = 1$ corresponds to a specialist for resource two (Fig. 1).

We consider five different trade-offs (listed in Table 2): (1) between the capture probability f_1 and f_2, (2) between the search efficiencies e_1 and e_2, (3) between the manipulation times t_{m1} and t_{m2}, (4) between the pursuit times t_{p1} and t_{p2}, and (5) between conversion efficiencies α_1 and α_2. Specialization for a certain resource i corresponds to an increase in $\alpha_i C_i$ (see Eq. 1). This is achieved when either t_{pi} or t_{mi} are decreasing or when f_i, e_i or α_i are increasing. Therefore we have to parameterize the trade-off curve in the opposite direction for t_{mi} and t_{pi} compared to f_i, e_i and α_i (see Fig. 1).

The curvature of the trade-off curve is determined by a parameter z in such a way that $z > 1$ gives rise to a convex phenotype set (bounded by weak trade-off) while $z < 1$ gives rise to a concave phenotype set (bounded by a strong trade-off) (Fig. 1). For numerical calculations we use one of the following parameterizations resulting in the trade-off curves of Fig. (1): for $\boldsymbol{x} \in \{\boldsymbol{\alpha}, \boldsymbol{e}, \boldsymbol{f}\}$ we use $\boldsymbol{x}(\theta) = (x_{1\max}(1-\theta)^{\frac{1}{z}}, x_{2\max}\theta^{\frac{1}{z}})$ while for $\boldsymbol{x} \in \{\boldsymbol{t_p}, \boldsymbol{t_m}\}$ we use $\boldsymbol{x}(\theta) = (x_{1\max} - x_{1\min}(1-\theta)^{\frac{1}{z}}, x_{2\max} - x_{2\min}\theta^{\frac{1}{z}})$, where $x_{1\min}, x_{1\max}, x_{1\min}, x_{2\min}$ are positive constants. Throughout the paper we use both vectors $\boldsymbol{x} = (x_1, x_2)$ and specialization coefficients θ, to characterize a pair of trait values lying on the trade-off curve.

2.3. Evolutionary Dynamics

A mutant differs from the resident in its position on the trade-off curve. A mutant phenotype is indicated by θ', giving rise to $\boldsymbol{x'} = (x_1', x_2')$. We assume that mutations are rare and of small effect. Because of the first assumption the ecological and evolutionary time scales are separated: a population has reached its ecological equilibrium before a new mutant arises. The fate of a mutant is determined by its invasion fitness, i.e., its per capita growth rate when it is still rare in a population dominated by a resident. For $\boldsymbol{x} \in \{\boldsymbol{f}, \boldsymbol{e}, \boldsymbol{t_m}, \boldsymbol{t_p}\}$ invasion fitness is given by

$$w(\theta', \theta) = \alpha_1 C_1(\theta', \hat{R}_1(\theta), \hat{R}_2(\theta)) + \alpha_2 C_2(\theta', \hat{R}_1(\theta), \hat{R}_2(\theta)). \tag{7}$$

If conversion efficiency $\boldsymbol{\alpha}$ is evolving, the α_i's are a function of θ' and not the functional responses C_i. Initially the mutant has no influence on the two resource levels. Therefore the resource levels are a function of the resident's trait value θ only. By $\hat{R}_i(\theta)$, we denote resource equilibria across years set by a consumer with trait value θ and equilibrium population $\hat{N}(\theta)$ (cf Eq. 6). Mutants with $w(\theta', \theta) > 1$ have a positive probability of invasion while mutants with $w(\theta', \theta) < 1$ are doomed to extinction. By definition, for any resident at population dynamical equilibrium $w(\theta, \theta) = 1$.

The direction of evolutionary change is derived from the fitness gradient, i.e., the first derivative of the fitness function (Eq. 7) with respect to the mutant's trait (see e.g. Geritz et al. 1998). Trait values θ^* where the fitness gradient equals zero are of special interest:

$$\left. \frac{\partial w(\theta', \theta^*)}{\partial \theta'} \right|_{\theta'=\theta^*} = 0. \tag{8}$$

Following Metz et al. (1996a) and Geritz et al. (1998) we call them evolutionarily singular points. Singular points θ^* can be classified according to two independent properties: convergence stability

and invadability (Geritz et al. 1998; Rueffler et al. 2004). The first property determines whether a singular trait value is reachable from nearby (Eshel 1983; Christiansen 1991; Abrams et al. 1993b; Geritz et al. 1998) while the second property determines whether any consumer with a different trait value than θ^* can increase in frequency when initially rare (Maynard Smith 1982). A singular trait value which is both convergence stable and uninvadable is called continuously stable strategy or CSS (Eshel and Motro 1981; Eshel 1983). It is a final stop of evolution. A convergence stable and invadable trait value is called evolutionary branching point (Metz et al. 1996a; Geritz et al. 1998). At these points selection becomes disruptive and favors increased genetic variation.

Note that traditional definitions of frequency-dependent selection have little discriminating power when applied to invasion fitness expressions as Eq. (7). In population genetics frequency-dependence is defined as the dependence of selection coefficients on allele frequencies. Invasion fitness does not consider this dependence since mutants are assumed to be rare and the frequency of the resident is always one. Lande's (1976) definition of frequency-dependence, as a dependence of fitness on the population mean trait value, includes all cases of density-dependent selection where a mutant's fitness depends on the equilibrium population size of the resident. In the following section we introduce the concept of the feedback environment and its dimensionality. This provides us with a tool to define frequency-dependence for density regulated populations as a condition allowing for rarity advantage and protected polymorphism.

3. Feedback Environment

Whether a certain mutation is beneficial or not depends on the trait value of the mutant and on the environment it experiences, which is set or influenced by the resident population. For example, if the probability of invasion of a mutant type is determined in direct contests with individuals of another common type, then those other individuals and their trait value can be viewed as the environment a mutant experiences. Fitness can be written as a function of the trait value of the mutant and of the resident: $w(\theta', \theta)$. In the model studied here, the interaction between individuals is not direct but indirect via competition for the same resources. In this case fitness is affected by the abundance of the resources (Eq. 7), which in turn are determined by the trait value of the resident type (Eq. 6). We refer to those components of the environment that mediate the interaction between individuals as feedback environment and collect them in a n-dimensional vector $\boldsymbol{I}$ (Heino et al. 1997, 1998; Diekmann et al. 2003; Meszéna et al. in revision). With a slight abuse of notation we can rewrite invasion fitness as a function of the mutant's trait value and the feedback environment $\boldsymbol{I}$ as it is determined by the trait value of the resident: $w(\theta', \boldsymbol{I}(\theta))$. The dimension n of the feedback environment indicates via how many different variables the interaction between resident and mutant is mediated. In the present case it seems intuitive to equate $\boldsymbol{I}$ with the two-dimensional vector $(\hat{R}_1, \hat{R}_2)$. If, however, by some mechanism $\hat{R}_1$ would always equal $\hat{R}_2$, then a scalar is sufficient to describe the feedback environment. The dimensionality of the feedback environment has important evolutionary consequences. Whenever the feedback environment can

be represented by a scalar, robust coexistence is impossible (Metz et al. 1996b; Meszéna et al. in revision). If, additionally, invasion fitness w is a monotone function in $\boldsymbol{I}$, then the evolutionary dynamics can be analyzed by maximizing an optimization criterion (Metz et al. 1996b). We call selection in one-dimensional feedback environments frequency-independent. On the contrary, if two or more variables are needed to describe the feedback environment, i.e., if $\boldsymbol{I}$ is a vector of dimension two or higher, fitness depends on the relative values of the interaction variables collected in $\boldsymbol{I}$ and optimization is generally impossible. We call selection in two- or higher-dimensional feedback environments frequency-dependent (compare Heino et al. 1998). We note that our definition differs from the classical definition of frequency-dependence as used in population genetics. In the next paragraph we show how a two-dimensional feedback environment allows for a rarity advantage and coexistence in protected polymorphisms.

4. Results

One of our main results is that the dimension of the feedback environment $\boldsymbol{I}$ depends on the trait that is considered to be evolvable. In order to illustrate the mechanism behind this result we derive it for the special (and easy) case that all traits that are not considered evolvable are symmetric. In Appendix B we prove the result for the general case without the symmetry assumption. Let us first assume that genetic variation occurs for $\boldsymbol{t_m}$, $\boldsymbol{t_p}$ and $\boldsymbol{\alpha}$ and not for $\boldsymbol{f}$ and $\boldsymbol{e}$. The symmetry assumption amounts to $f_1 = f_2$, $e_1 = e_2$, $b_1 = b_2$ and $d_1 = d_2$. Given this symmetry, we immediately see from Eq. (6) that $\hat{R}_1 = \hat{R}_2$, independent of the amount of genetic variation and of the degree of asymmetry in the traits $\boldsymbol{t_m}$, $\boldsymbol{t_p}$ and $\boldsymbol{\alpha}$. The reason for this effect is that these traits influence both resource equilibria in the same way via the consumer density N and the search probability s. A population that is completely specialized on resource one in terms of these traits (i.e., $t_{m1} \ll t_{m2}$, $t_{p1} \ll t_{p2}$, $\alpha_1 \gg \alpha_2$) does not cause resource one to be more depleted than resource two. Let us now investigate the case where evolution occurs for $\boldsymbol{f}$ or $\boldsymbol{e}$ and not for the other variables. These traits do have a resource specific effect (see Eq. 6). If $f_1 > f_2$ or $e_1 > e_2$, then $\hat{R}_1$ will be lower than $\hat{R}_2$ and vice versa (see Eq. 6). Hence, in this case we need two scalars in order to track changes in the resource equilibria while the consumer population evolves. We can now easily see how the dimension of the feedback environment affects the possibility for frequency-dependence. If specialization in the consumer makes the resource it preys upon more effectively less abundant, then a mutant that specializes on an underused resource will enjoy a rarity advantage. This mechanism clearly does not work in one-dimensional feedback environments where specialization in the consumer has no resource specific effects.

4.1. Traits With Two-Dimensional Feedback Environment

We start with the traits of this category because they directly correspond to the traits considered by Lawlor and Maynard Smith (1976), Lundberg and Stenseth (1985), Abrams (1986) and

Wilson and Turelli (1986). Only the evolution of capture probability $\boldsymbol{f}$ is described in detail since the results for search efficiency $\boldsymbol{e}$ are qualitatively identical.

Invasion fitness is given by Eq. (7) with

$$C_i = \frac{e_i \hat{R}_i f_i'}{1 + e_1 \hat{R}_1 (t_{p1} + f_1' t_{m1}) + e_2 \hat{R}_2 (t_{p2} + f_2' t_{m2})}. \tag{9}$$

Given some symmetry constraints we can prove that the evolutionary dynamics of capture probability $\boldsymbol{f}$ and search efficiency $\boldsymbol{e}$ are driven by the effect of mutations on the linear terms of the functional response (see Appendix A). This result is confirmed numerically for cases where the symmetry constraints are not met. It is therefore sufficient to study a fitness function derived from a linear functional response:

$$w(\boldsymbol{f'}, \boldsymbol{f}) = \alpha_1 e_1 \hat{R}_1 f_1' + \alpha_2 e_2 \hat{R}_2 f_2', \tag{10}$$

which is equivalent to the ones studied by the authors referred to at the beginning of this section.

Fig. 2a shows the evolutionary dynamics as a function of the parameter z, the strength of the trade-off curve. The figure is based on numerical calculations where all parameters besides $\boldsymbol{f}$ are assumed to be equal for both resources. In Appendix A we show that the qualitative pattern can be derived partly analytically. Asymmetric parameter values do not change the results qualitatively but merely lead to asymmetries in Fig. (2). ere we give a verbal explanation of the results. When the trade-off is weak ($z > 1$), the generalist's trait is a global attractor of the evolutionary dynamics and once it is reached it cannot be invaded by any other mutant. Hence, it is a unique CSS. The mechanism behind this dynamics is as follows. Mutants that are more similar to the generalist than the resident in terms of their capture probabilities are able to invade. Such mutants benefit in two ways. (i) Because of the weak trade-off mutants closer to the generalist have a higher overall capture probability than the resident. By overall capture probability we mean the sum of the resource specific capture probabilities weighted by the traits assumed to be constant, hence: $\alpha_1 e_1 f_1' + \alpha_2 e_2 f_2' > \alpha_1 e_1 f_1 + \alpha_2 e_2 f_2$. When α_i and e_i are equal for both resources this sum has a maximum at the generalist's trait value with $f_1 = f_2$. (ii) As explained in the preceding section, a resident that is specialized in terms of its capture probability on one resource causes that resource to be relatively rare compared to the resource it is not specialized on. Mutants that are more similar to the generalist benefit in such a situation since they make better use of the less exploited resource while decreasing their success on the more exploited resource. We want to emphasize that it is this second feature which introduces frequency-dependence into the fitness of the mutant. Once the generalist is predominant, it cannot be invaded anymore since any possible mutant would have a lower overall capture probability while no rarity advantage exists since both resource are equally abundant.

When the trade-off is strong ($z < 1$), the trait value of the generalist is still convergence stable, however, in contrast with the preceding scenario, it loses its uninvadability when predominant and

therefore turns into a branching point. With a strong trade-off, a mutant that is more similar to the generalist suffers a loss in its overall capture probability since this sum now has a minimum at the trait value of the generalist. This imposes a selection component towards further specialization. However, overall, the generalist remains attracting as long as the gain from becoming more specialized on the underused resource more than outweighs the loss from a decrease in overall capture probability. Once the generalist is predominant any mutant can invade. In this situation a mutant that is deviating from the generalist benefits from an increase in its overall capture probability on resources that are equally abundant. However, when the mutant increases in frequency, the resource that it captures more efficiently becomes less common. This gives a benefit to the generalist again. The mutant does not go to fixation and the two types can coexist in a protected polymorphism. Subsequently, only mutants that are more specialized than either of the two residents are able to invade. This is a phase of character displacement driven by resource competition. In case of haploid organisms, the dimorphic evolution results in a pair of two resident types, each completely specialized on one resource. This can be derived from the geometrical argument presented in Rueffler et al. (2004) and is also described by Lawlor and Maynard Smith (1976).

The basin of attraction of the generalist, that is, the range of initial trait values from which populations converge towards the generalist's trait over evolutionary time, decreases with increasing strength of the trade-off (i.e., with lower values of z). For very strong trade-offs only populations that already perform reasonably well on both resources, will evolve towards the generalist (Fig. 2a). When the initial population is relatively specialized on one resource, selection will drive it towards further specialization. In this situation the gain of further specialization due to an increase in overall capture probability more than compensates for the detrimental effect of improving on an already over-exploited resource. Though in this case a polymorphism cannot emerge by small mutational steps at a branching point, coexistence is possible for types that are sufficiently different from each other. This can for instance be the case when immigrants specialized for one resource enter a population of specialists for the other resource. For very strong trade-offs ($z \ll 1$) the generalist may even turn into an evolutionary repellor. However, for parameters we checked, the repellor lies in a parameter region where the population is not viable (see Fig. 2a).

Invasion fitness for search efficiency e is given by Eq. (7) and (9) where the e_i's are labeled by a dash instead of the f_i's. Obviously the structure of the fitness function does not change and therefore it results in the same bifurcation diagram (Fig. 2a).

4.2. Traits With One-Dimensional Feedback Environment

As in the previous section, we will describe the dynamics of one trait, manipulation time t_m, in detail. The other two traits belonging to the same category, pursuit time t_p and conversion efficiency α, show qualitatively identical evolutionary dynamics.

In contrast to the traits in the previous section, a mutation in t_m only affects the denominator

of the functional response C_i and hence search probability s (see Eq. 3). Invasion fitness is given by

$$w(\boldsymbol{t'_m}, \boldsymbol{t_m}) = s'(\alpha_1 e_1 \hat{R}_1(\boldsymbol{t_m}) f_1 + \alpha_2 e_1 \hat{R}_2(\boldsymbol{t_m}) f_2) \tag{11}$$

with

$$s' = 1 / \left(1 + e_1 \hat{R}_1(t_{p1} + f_1 t'_{m1}) + e_2 \hat{R}_2(t_{p2} + f_2 t'_{m2})\right). \tag{12}$$

The evolutionary dynamics for manipulation time are shown in Fig. 2b. For weak trade-offs ($z > 1$) the generalist with $t_{m1} = t_{m2}$ is again a unique CSS while for strong trade-offs ($z < 1$) the generalist turns into an evolutionary repellor. In this case the degree of specialization of the initial population decides whether selection leads to complete specialization on resource one or resource two. The mechanism behind this is simple. Any mutant with $s' > s$ (Eq. 3) has $w(\boldsymbol{t'_m}, \boldsymbol{t_m}) > 1$ and is therefore able to invade. This is equivalent to demanding $e_1 \hat{R}_1 f_1 t'_{m1} + e_2 \hat{R}_2 f_2 t'_{m2} < e_1 \hat{R}_1 f_1 t_{m1} + e_2 \hat{R}_2 f_2 t_{m2}$. Given that the two resource equilibria $\hat{R}_1$ and $\hat{R}_2$ are equal (as it is the case when all fixed parameters are symmetric), evolution minimizes $e_1 f_1 t'_{m1} + e_2 f_2 t'_{m2}$. For weak trade-offs, the generalist minimizes this weighted sum while for strong trade-offs the two specialists correspond to minima. A mutant can enjoy an advantage when it has increased its search probability s and therefore can live on fewer resources than the resident but not because it is rare. At the bifurcation point ($z = 1$) the fitness landscape is completely flat and all traits are selectively neutral, indicated by a vertical line in Fig. 2b. However, this degeneracy only occurs when symmetric parameter values are assumed. The fact that at the bifurcation of a CSS into a repellor two independent properties, convergence stability and invadability, change simultaneously, is the due to the absence of frequency-dependence.

Though these results are in accordance with the predictions based on Levins' fitness set approach, we can in general not use his methodology to achieve them. Only under the assumption of symmetry in certain parameters we are able to derive an optimization principle (see Appendix B), which is equivalent to what Levins called the adaptive function.

The fitness function for pursuit time is structurally identical to Eq. (11) and Eq. (12) and therefore shows a qualitatively identical bifurcation pattern (Fig. 2b). When mutations affect $\boldsymbol{\alpha}$ invasion fitness is given by $w(\boldsymbol{\alpha'}, \boldsymbol{\alpha}) = \alpha'_1 C_1 + \alpha'_2 C_2$ with C_i as in Eq. (2). Although the fitness function is structurally different, it results in the same bifurcation pattern as in the preceding cases and we are again able to derive an optimization principle when certain parameters are symmetric (see Appendix B).

5. Discussion

In this paper we analyzed a model for the evolutionary dynamics of five different foraging related traits of a consumer feeding on two resources. Similar models have been used extensively in the study of character displacement between two competing consumer types (MacArthur and Levins 1964; Lawlor and Maynard Smith 1976; Lundberg and Stenseth 1985; Abrams 1986). Here

we concentrate on the evolution of a consumer population consisting of only one type. Our main results are that the evolutionary dynamics of such a monomorphic population can differ strongly for different traits (Fig. 2, Tab. 2) and that for some traits polymorphisms can emerge through a series of mutations of small effect while for others coexistence of different types is generically impossible.

At a first glance the different traits considered to be subject to evolutionary change seem to be mechanistically similar and the discovered dichotomy in the evolutionary dynamics was to our knowledge not recognized previously. However, there seems to be a certain awareness at least since the early 70th that coexistence cannot be mediated by just any trait. For instance, from MacArthur's competition coefficient (e.g. MacArthur 1972; Schoener 1974), one can infer that for a model with linear functional response, coexistence is only possible if consumers differ in their search efficiencies and that differences in conversion efficiency are not sufficient. Vincent et al. (1996) found similar results for a model with type II functional response: types that only differ in either handling time or conversion efficiency cannot coexist on an ecological time scale while differences in search efficiency do suffice to mediate coexistence. Whether a trait can mediate coexistence or not reflects whether it causes interactions to be frequency-dependent or not. It is this perspective that allows us to gain insight into the mechanism of how different traits affect coexistence.

If selection is frequency-dependent, i.e., in case of capture probability f and search efficiency e, polymorphisms can emerge from a monomorphic population at an evolutionary branching point. This happens for moderately strong trade-offs. In this case a mutant that is approaching the generalist's trait value is able to invade. Such a mutant gains from improving on the underused resource and this directional force towards the generalist is stronger than the disruptive force stemming from the strong trade-off. This is the mechanism discovered by Wilson and Turelli (1986) in the case of marginal underdominance, where a rare heterozygote corresponding a generalist invades a resident homozygote corresponding to a specialist. We showed that evolution towards the generalist can occur through a series of small mutational steps. Convergence towards the generalist with subsequent disruptive selection was not recognized by Lawlor and Maynard Smith (1976) and Abrams (1986), because strong trade-offs were a priori identified with immediate specialization. Lundberg and Stenseth (1985) formulated a population genetics version of the model of Lawlor and Maynard Smith where they explicitly considered the evolution of a single consumer. They also postulated immediate specialization in connection with strong trade-offs because they overlooked the variable character of the fitness landscape with changing gene frequencies. Following the classical tradition, they envisage evolution on a fitness landscape that corresponds to equilibrium gene frequencies and not corresponding to the present gene frequency (in the adaptive function (their Eq. 14) the resource levels corresponding to the gene frequency of the resident population have to be inserted instead of the resource levels corresponding to the equilibrium gene frequency). Diekmann et al. (2005) investigate a very similar model where the trade-off is in the uptake coefficients for two different resources. Their model assumes clonal reproduction as well, but leaves out the assumption that mutations are necessarily rare, with a narrow, continuous distribution of trait

values as a result. They also find that evolutionary branching occurs for strong trade-offs.

Evolutionary change in the other three traits, pursuit time t_p, manipulation time t_m and conversion efficiency of resources into offspring α, is not subject to frequency-dependent selection. In these cases an optimal consumer exists that is favored by selection over all other possible types and generically only one consumer can exist on two different resources. If the trade-off is weak, the optimal trait value corresponds to a generalist and if the trade-off is strong, the optimal trait value corresponds to either of the two specialists with the outcome depending on initial conditions. Though these predictions are in accordance with those derived by Levins (1962), we want to emphasize that we could generally not fall back on Levins' approach. Only under some symmetry assumptions did we succeed to derive optimization principles which are essential elements of Levins' methodology.

Our results show that two aspects are decisive for the evolutionary dynamics of foraging traits: the shape of the trade-off and the dimension of the feedback environment. If one wants to relate our results to real organisms these features have to be studied. Considerable effort has been made with respect to the shape of the trade-off (Benkman 1993; Schluter 1993, 1995; Robinson et al. 2000) though is is only recently that more powerful methods are developed to infer the shape from empirical data (Hatfield and Schluter 1999; O'Hara Hines et al. 2004). The tendency in the cited studies is that trade-offs are indeed rather strong than weak, which fulfils a necessary requirement for diversification in our theory.

Two extensions of the presented model seem obvious. Firstly, foraging related traits without doubt do not evolve separately as envisaged in our model but simultaneously. Simultaneous evolution of several traits will alter the results at least quantitatively. For instance, a decrease in handling time for a certain resource will be accompanied by an increase in search efficiency and capture probability. We can therefore expect that the feedback environment generally is not one-dimensional. Secondly, like all our predecessors, we assumed that the consumer does not choose between different prey. Upon encounter the consumer always attacks both types of prey, regardless of its degree of specialization for one prey or the other. Abrams (1986) remarks that strongly asymmetric handling times are expected to cause exclusion of one resource from the diet with specialization for the remaining one as a consequence. Hence, strong interactions result between the evolutionary dynamics of morphological and physiological traits on the one hand and behavioral traits such as diet choice that can change on an ecological times scale on the other hand. These interactions will be the subject of a follow-up paper.

To summarize, our results show that depending on the trait that is considered to evolve, selection is either frequency-dependent or frequency-independent in the same ecological system. For these two cases the evolutionary dynamics of specialization can be in opposite directions. While a monomorphic population subject to frequency-dependent selection and with a strong trade-off evolves towards the generalist's trait value, the same population will evolve towards a specialist for a trait not subject to frequency-dependent selection. Under frequency-dependent selection,

a monomorphic population can split at an evolutionary branching point. If the genetic system and/or mating system does not favor the production of intermediate phenotypes, or if a mechanism evolves that disfavors the production of such types, subsequent evolution will lead to a dimorphic population exclusively consisting of two specialists.

Acknowledgments

A. Analytical Results

Given the symmetries $\alpha_1 = \alpha = \alpha_2$ and $t_{m1} = t_m = t_{m2}$ we can prove that the evolutionary dynamics of capture probability $\boldsymbol{f}$ is driven by the effects of mutations on the linear terms of the functional response. To show this, we take the derivative of Eq. (7) with respect to f_1':

$$\frac{\partial w(\boldsymbol{f}', \boldsymbol{f})}{\partial f_1'} = \frac{\alpha \left(e_1 \hat{R}_1 + e_2 \hat{R}_2 \frac{\mathrm{d} f_2'}{\mathrm{d} f_1'}\right)\left(1 + e_1 \hat{R}_1 t_{p1} + e_2 \hat{R}_2 t_{p2}\right)}{\left(1 + e_1 \hat{R}_1(t_{p1} + f_1 t_m) + e_2 \hat{R}_2(t_{p2} + f_2 t_m)\right)^2} \tag{A1}$$

The sign of this derivative is solely determined by the first term in brackets in the numerator. This is exactly the derivative of the fitness function with linear functional response. Numerical explorations show that the qualitative behavior of the model, i.e., the number and type of singular points, does not change if we break the above symmetry constraints. A similar argument holds for search efficiency $\boldsymbol{e}$.

The bifurcations shown in Fig. 2 are calculated numerically. Here we derive analytical results to underpin the robustness of the numerical results. From a geometrical argument presented in Rueffler et al. (2004), we can derive that weak trade-offs only allow for uninvadable singular points (CSSs and Garden of Eden points) while strong trade-offs only allow for invadable singular points (repellors and branching points). The prerequisite for this conclusion is that those trait combinations (x, y), that are initially selectively neutral with respect to a given resident trait value lie on a straight line in the (f_1, f_2)-plane. We call such lines invasion boundaries. They are implicitly given by the fitness function (Eq. 7) set equal to one, i.e.:

$$1 = \frac{\alpha e_1 \hat{R}_1 x + \alpha e_2 \hat{R}_2 y}{1 + e_1 \hat{R}_1(t_{p1} + x t_m) + e_2 \hat{R}_2(t_{p2} + y t_m)}, \tag{A2}$$

which after rearranging becomes a linear equation in x with a negative slope:

$$y = \frac{1 + e_1 \hat{R}_1 t_{p1} + e_2 \hat{R}_2 t_{p2}}{e_2 \hat{R}_2 (\alpha - t_m)} - x \frac{e_1 \hat{R}_1}{e_2 \hat{R}_2}. \tag{A3}$$

It is easy to show that $(\alpha - t_m) > 0$ is a necessary prerequisite for a viable population. Hence, Eq. (A3) has a positive intercept.

Setting Eq. (A1) equal to zero gives us a characterization of singular points $\boldsymbol{f}^*$:

$$\frac{\mathrm{d} f_2}{\mathrm{d} f_1} = -\frac{e_1 \hat{R}_1}{e_2 \hat{R}_2}. \tag{A4}$$

Under the additional symmetry constraints that $x_1 = x = x_2$ for $\boldsymbol{x} \in \{\boldsymbol{e}, \boldsymbol{b}, \boldsymbol{d}\}$ and the assumption that $f_1 = f_2$ implies $\mathrm{d} f_2/\mathrm{d} f_1 = -1$, this is fulfilled for (f_1^*, f_2^*) with $f_1^* = f_2^*$. In a next step we show that such a intermediate singular point is a unique CSS for weak trade-offs. From $(f_1 \lessgtr f_1^*) \Rightarrow (\mathrm{d} f_2/\mathrm{d} f_1 \gtrless -1)$ and $(f_1 \lessgtr f_1^*) \Rightarrow (\hat{R}_1 \gtrless \hat{R}_2)$ follows $(f_1 \lessgtr f_1^*) \Rightarrow (\hat{R}_1 + \mathrm{d} f_2/\mathrm{d} f_1 \hat{R}_2 \gtrless 0)$.

Hence, the fitness gradient is positive when $f_1 < f_1^*$ and negative when $f_1 > f_1^*$. This means that $\boldsymbol{f}^*$ is a globally attracting and unique CSS.

As mentioned above the CSS loses its uninvadability when the trade-off becomes strong. Generically, a CSS becoming invadable turns into a branching point (Metz et al. 1996a; Geritz et al. 1998; Rueffler et al. 2004). For our trade-off parameterization it is easy to show that the boundaries of the trait space are attracting in case of strong trade-offs. Consequently, a repellor has to exist between the boundaries and the intermediate branching point. Numerical calculations reveal a pitchfork bifurcation. It follows from standard bifurcation theory that a pitchfork bifurcation unfolds into a fold bifurcation when asymmetries in the parameters are introduced.

B. Dimension of the Feedback Environment and Optimization

Fitness is a function both of a specific phenotype and its environment. In order to make this point operational the term "environment" has to be defined formally. The feedback environment $\boldsymbol{I}$ is a n-dimensional vector that contains information on those aspects of the environment that are affected by a focal population and simultaneously feed back by determining the current selection pressure that is acting on the population. Due to this eco-evolutionary feedback loop, the environment in a sense co-evolves with the traits in the population. On an ecological time scale, the defining property of the feedback environment is that individuals become independent of each other when the feedback is given as a function of time (Diekmann et al. 2003; Meszéna et al. in revision). On an evolutionary time scale $\boldsymbol{I}$ depends on the types present in the population and on a population dynamical attractor of that population. $\boldsymbol{I}$ then contains the minimum number of scalars that is needed to make the growth rate of a focal individual independent of the resident population. The dimension of $\boldsymbol{I}$ indicates via how many different environmental components the interaction between individuals is mediated and $\dim(\boldsymbol{I})$ constitutes an upper limit for the number of potentially coexisting types (e.g. Meszéna et al. in revision).

In the present model the interactions between individuals are mediated by the densities of the two resources $\hat{R}_1$ and $\hat{R}_2$. The upper limit for $\boldsymbol{I}$ and for the number of possibly coexisting types is therefore two. Here we show that the dimension of $\boldsymbol{I}$ reduces to one when individuals are only allowed to differ in $\boldsymbol{t_p}, \boldsymbol{t_m}$ and $\boldsymbol{\alpha}$, as it is the case when we consider evolution in these traits in populations monomorphic in $\boldsymbol{e}$ and $\boldsymbol{f}$. To see this, let us consider a mutant θ' with manipulation time $\boldsymbol{t'_m}$ that is invading a resident community consisting of the two phenotypes θ^1 and θ^2 (the maximum number that can possibly coexist) with corresponding manipulation times $\boldsymbol{t_m^1} = (t_{m1}^1, t_{m2}^1)$ and $\boldsymbol{t_m^2} = (t_{m1}^2, t_{m2}^2)$, respectively, resulting in the search probabilities s^1 and s^2 and equilibrium consumer densities $\hat{N}^1$ and $\hat{N}^2$. Superscripts refer to consumer types while subscripts refer to resources specific traits. We can derive $\boldsymbol{I}$ from the fitness function of the mutant: $w(\theta', \boldsymbol{I}(\theta^1, \theta^2))$. This function is given by Eq. (7) with the difference that the resource equilibria

are determined by the two resident phenotypes simultaneously (cf Eq. 6):

$$\hat{R}_i(\theta^1, \theta^2) = \frac{b_i}{d_i + e_i f_i(s^1 \hat{N}^1 + s^2 \hat{N}^2)} \qquad \text{for} \qquad i \in \{1, 2\}. \tag{B1}$$

Note that the different traits t^i_{mj} influence the resource equilibria only through the search probabilities s^i and the consumer densities $\hat{N}^i$. From Eq. (B1) we can see that it is sufficient to consider $\sum_{i=1}^2 s^i \hat{N}^i$ as a function of time in order to achieve independence between the growth rate of an individual and the resident community. This is a scalar and hence $\boldsymbol{I}$ is one-dimensional. The same holds true if the population is polymorphic in either $\boldsymbol{t}_p$ or $\boldsymbol{\alpha}$. Note, that populations that are polymorphic in all three of these traits simultaneously still correspond to a one-dimensional $\boldsymbol{I}$.

If the resident population is polymorphic in the capture probabilities, say, $\boldsymbol{f}^1 = (f_1^1, f_2^1)$ and $\boldsymbol{f}^2 = (f_1^2, f_2^2)$, then the resource equilibria are given by:

$$\hat{R}_1(\theta^1, \theta^2) = \frac{b_1}{d_1 + e_1(f_1^1 s^1 \hat{N}^1 + f_1^2 s^2 \hat{N}^2)}$$
$$\hat{R}_1(\theta^1, \theta^2) = \frac{b_2}{d_2 + e_2(f_2^1 s^1 \hat{N}^1 + f_2^2 s^2 \hat{N}^2)}.$$

Since the capture probabilities do have a resource specific impact, we need to specify two numbers in order to achieve independence between individuals: $\boldsymbol{I} = (\sum_{i=1}^2 f_1^i s^i \hat{N}^i, \sum_{i=1}^2 f_2^i s^i \hat{N}^i)$. Hence, the $\boldsymbol{I}$ vector does not reduce to a scalar but remains two-dimensional. The same result holds for search efficiency $\boldsymbol{e}$.

A consequence of a one-dimensional $\boldsymbol{I}$-vector is that coexistence of two types is impossible. This can be seen from the following argument (see also Meszéna et al. (in revision)). At population dynamical equilibrium of two species with trait values θ^1 and θ^2

$$1 = w\left(\theta^i, \boldsymbol{I}(\theta^1, \theta^2)\right) \quad \text{for} \quad i \in 1, 2. \tag{B2}$$

For an arbitrary combination of two trait values, solving the system of equations (B2) for a one-dimensional $\boldsymbol{I}$ amounts to solving a system of two equations in one unknown. Hence, no generic solution exists. By contrast, in case of two dimensions, Eq. (B2) is a system of two equations in two unknowns, which can have a robust solution.

A one-dimensional feedback loop is a necessary prerequisite for the existence of an optimization criterion (Metz et al. 1996b). However, we are able to find explicit optimization criteria only when some symmetry constraints are met. When it is possible to collect those parameters of the fitness function that are determined by resident and by the mutant in different factors, we can obtain an optimization principle. Let us consider the case of manipulation time $\boldsymbol{t_m}$. A mutation only affects search probability s. If $e_1 = e = e_2$, $f_1 = f = f_2$ and $d_1 = d = d_2$, we can rewrite Eq. (12) after some rearrangement as

$$s' = \frac{1}{1 + \frac{e}{d + sef\tilde{N}(\boldsymbol{t_m})}\left[f(b_1 t'_{m1} + b_2 t'_{m2}) + (b_1 t_{p1} + b_2 t_{p2})\right]}. \tag{B3}$$

Any mutant with $b_1 t'_{m1} + b_2 t'_{m2}$ smaller than the resident, is able to invade and a value of θ that minimizes this sum cannot be invaded by any mutant and therefore corresponds to a CSS. Note, that in deriving the optimization criterion in this way we do not need symmetry in $\boldsymbol{b}$ (compare Section 4.2). From the same equation we see that in the case of pursuit time $\boldsymbol{t_p}$ we have to minimize $b_1 t'_{p1} + b_2 t'_{p2}$ in order to find CSS's.

With the same symmetry constraint we can rewrite the invasion fitness for $\boldsymbol{\alpha}$ as

$$w(\boldsymbol{\alpha}', \boldsymbol{\alpha}) = s \frac{ef}{d + sef\hat{N}(\boldsymbol{\alpha})} (\alpha'_1 b_1 + \alpha'_2 b_2). \tag{B4}$$

It follows that $\alpha_1 b_1 + \alpha_2 b_2$ acts as an optimization criterion.

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Table 1: Notation. The index i refers to one out of two possible resources.

Term	Definition
α_i	conversion efficiency of consumed resource into offspring
b_i	constant resource influx
C_i	consumer's functional response
d_i	death rate of resource
e_i	consumer's search efficiency [area/ time step]
f_i	capture probability for an attacked resource item
N_t	consumer population density at time step t
p_i	consumer's probability of attack upon encounter with resource
R_i	resource density [1/area]
t_{mi}	manipulation time (needed for treatment of an already capture resource item)
t_{pi}	pursuit time (needed catch an attacked resource item)
s	search probability (fraction of time spent searching for resources)
θ	specialization coefficient $\in [0,1]$, determines location on the trade-off curve
w	invasion fitness
z	strength of trade-off ($z > 1$ strong, $z = 1$ linear, $z < 1$ weak)

Table 2: Overview of traits considered evolvable. Each parameter stands for a vector of two traits coupled by trade-off.

Trait		Dimension of Feedback Environment $\boldsymbol{I}$	Selection
conversion efficiency	$\boldsymbol{\alpha}$	one	frequency-independent
search efficiency	$\boldsymbol{e}$	two	frequency-dependent
capture probability	$\boldsymbol{f}$	two	frequency-dependent
manipulation time	$\boldsymbol{t_m}$	one	frequency-independent
pursuit time	$\boldsymbol{t_p}$	one	frequency-independent

Fig. 1.— Trade-off curves for capture probability $\boldsymbol{f}$ (a) and manipulation time $\boldsymbol{t_m}$ (b). The number next to each curve is the parameter z determining the strengh of the trade-off. Note that for capture probability the phenotype set (i.e., the set of possible phenotypes) lies below the trade-off curve and that the opposite holds true for manipulation time. The trade-off curve is parameterized in such a way that $\theta = 0$ corresponds to a specialist for resource one, and $\theta = 1$ corresponds to a specialist for resource two. Therefore the two trade-off curves are parameterized in opposite direction. All filled circles half way on the trade-off curve correspond to the generalist with $\theta = 0.5$. Other parameter values: $\boldsymbol{t_{m\text{max}}} = (1, 1)$, $\boldsymbol{t_{m\text{min}}} = (0.5, 0.5)$, $\boldsymbol{f_{\text{max}}} = (1, 1)$.

Fig. 2.— Bifurcation diagrams for capture probability $\boldsymbol{f}$ (a) and manipulation time $\boldsymbol{t_m}$ (b). Lines indicate the location and type of evolutionarily singular values of the specialization coefficient θ as a function of the bifurcation parameter z, the strength of the trade-off curve. Arrows give the direction of evolutionary change. The hatched area indicates parameter combinations corresponding to non-viable populations. Other parameter values: for (a) & (b) $\boldsymbol{\alpha} = (1, 1)$, $\boldsymbol{t_p} = (0.1, 0.1)$, $\boldsymbol{e} = (0.05, 0.05)$, $\boldsymbol{b} = (5000, 5000)$, $\boldsymbol{d} = (0.1, 0.1)$; only for (a) $\boldsymbol{f_{\text{max}}} = (1, 1)$, $\boldsymbol{t_m} = (0.1, 0.1)$; only for (b) $\boldsymbol{f} = (1, 1)$, $\boldsymbol{t_{m\text{min}}} = (0.5, 0.5)$, $\boldsymbol{t_{m\text{max}}} = (1, 1)$. See text for further explanation.

Figure (1)

Figure (2)