

EVOLUTION OF SPECIALIZATION AND ECOLOGICAL CHARACTER DISPLACEMENT OF HERBIVORES ALONG A GRADIENT OF PLANT QUALITY

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Abstract.—We study the combined evolutionary dynamics of herbivore specialization and ecological character displacement, taking into account foraging behavior of the herbivores, and a quality gradient of plant types. Herbivores can adapt by changing two adaptive traits: their level of specialization in feeding efficiency and their point of maximum feeding efficiency along the plant gradient. The number of herbivore phenotypes, their levels of specialization, and the amount of character displacement among them are the result of the evolutionary dynamics, which is driven by the underlying population dynamics, which in turn is driven by the underlying foraging behavior. Our analysis demonstrates broad conditions for the diversification of a herbivore population into many specialized phenotypes, for basically any foraging behavior focusing use on highest gains while also including errors. Our model predicts two characteristic phases in the adaptation of herbivore phenotypes: a fast character-displacement phase and a slow coevolutionary niche-shift phase. This two-phase pattern is expected to be of wide relevance in various consumer-resource systems. Bringing together ecological character displacement and the evolution of specialization in a single model, our study suggests that the foraging behavior of herbivorous arthropods is a key factor promoting specialist radiation.

Key words.—Adaptive dynamics, adaptive radiation, coevolutionary niche shift, ecological character displacement, foraging behavior, herbivorous arthropods, resource gradient.

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Most herbivorous arthropods exploit one or a few plant species (Jaenike 1990; Schoonhoven et al. 1998). Why such specialists dominate is a major question (Berenbaum 1996). It is generally assumed that herbivores face a trade-off in using different host plants. Thus, a specialist gains fitness on one host plant at the expense of fitness on others, whereas a generalist is a jack of all trades, but master of none (Levins 1962, 1968; MacArthur and Levins 1964; Lawlor and Maynard Smith 1976; Rosenzweig 1981, 1987; Brown and Pavlovic 1992). Specialization is traditionally predicted to evolve under a strong trade-off, that is, when density-independent fitness of a specialist on its resource is higher than that of a generalist on all resources combined (Levins 1962, 1968). However, when optimal foraging (or adaptive habitat choice) is included, specialization is even selected for under a weak trade-off (i.e., when a specialist gains less than it loses on other hosts), because inferior resources are avoided (Rosenzweig 1981, 1987; Wilson and Yoshimura 1994; Egas et al. 2004).

The models cited above did not explicitly consider the evolutionary dynamics of specialization. Adaptive dynamics theory provides tools for studying such processes in their proper frequency-dependent context (Metz et al. 1992, 1996a; Dieckmann and Law 1996; Dieckmann 1997; Geritz et al. 1998), by explicitly allowing ecological feedback into the evolutionary process (Heino et al. 1998). Evolutionary models of this type have highlighted how directional selection may drive a population toward a regime of disruptive selection, promoting adaptive radiation and speciation (Doebeli 1996; Geritz et al. 1998; Dieckmann and Doebeli 1999; Doebeli and Dieckmann 2000, 2003; Geritz and Kisdi 2000;

Dieckmann et al. 2004; see also Rosenzweig 1978; Christiansen 1991; Brown and Pavlovic 1992; Abrams et al. 1993a).

In this article, we extend previous evolutionary models of herbivore specialization by enhancing them with a combination of two key features. First, we include a continuum of plant types, which can be arranged along a nonspatial quality gradient, instead of considering only two discrete resources. Second, we allow errors in herbivore foraging that inevitably result, for example, from sampling the environment or from sensory constraints (Stephens and Krebs 1986). Both extensions are inspired by what is known about the ecology of insect herbivores. Plants may exhibit gradients in concentration of toxic or nutritive compounds, and insect herbivores are certainly not omniscient, nor do they move cost-free or redistribute instantaneously (Kennedy and Gray 1993). Thus, central assumptions underlying existing models of specialization are generally violated in nature (e.g., Ward 1987, 1992; Mayhew 1997; Grünbaum 1998; Schoonhoven et al. 1998).

These extensions enable an analysis that addresses the intricate coupling between relatively realistic renditions of three key biological processes, operating at different time scales (Fig. 1): evolutionary dynamics (slow pace; with our model accounting for both frequency- and density-dependent selection), population dynamics (intermediate pace; accounting for a full gradient of plant types), and behavioral dynamics (fast pace; accounting for inevitable errors in foraging activity).

By including a gradient of plant resources, we link the evolution of specialization to ecological character displacement, that is, to the process by which natural selection on

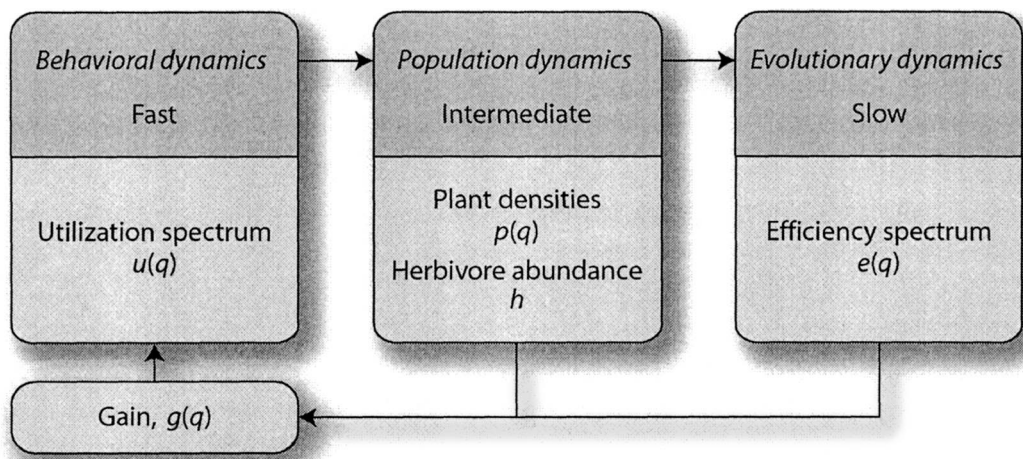


FIG. 1. Our model describes the interplay between processes at three different time scales. At the fast behavioral time scale, herbivores forage and adjust their utilization spectrum $u(q)$ along the gradient of plant qualities q . At the intermediate population dynamical time scale, plant densities $p(q)$ and herbivore abundances h are changing. At the slow evolutionary time scale, the physiology of herbivores adapts, resulting in modifications of their efficiency spectrum $e(q)$. A feedback to the behavioral dynamics occurs because population dynamics and evolutionary dynamics affect the gain $g(q)$ that a herbivore can extract from plant quality q , leading to altered utilization.

competing species in a community (or phenotypes in a population) leads to increased differences in the distribution of a quantitative character along a resource axis (Slatkin 1980). Three aspects, mostly neglected by the many preceding studies on character displacement, are addressed in this article.

First, most earlier studies investigated character displacement using ecological or quantitative genetic models with a fixed number of species (e.g., MacArthur and Levins 1967; May and MacArthur 1972; Roughgarden 1972; Slatkin 1980; Case 1981; Taper and Case 1985; for a review, see Taper and Case 1992b). Rummel and Roughgarden (1983, 1985), and Taper and Case (1992a,b) extended this approach by investigating whether there is room for an additional species at the coevolutionary equilibrium of a fixed number of species. These studies allowed invasion of a new species by migration from outside the coevolved system to increase the number of species (the fact that Rummel and Roughgarden's model allows for interspecific but not intraspecific frequency-dependent selection casts doubt on some of their results; see review in Taper and Case 1992b). Brown and Vincent (1992) studied evolutionarily stable states of a predator-prey model, explicitly allowing for multiple species, without investigating, however, the selection pressures that would favor an increased number of species. In contrast, our model allows the emergence of new phenotypes when there is selection for a phenotype to split in two (i.e., when a phenotype comes under disruptive selection; migration will not be considered in our model). Accordingly, the number of species/phenotypes in our model is an emergent property of the population dynamical feedback into the evolutionary process.

Second, most earlier models of character displacement studied evolution of the distance between niches along a resource gradient, but limited attention to settings in which the niche width of species was kept constant (e.g., Slatkin 1980; see the review in Taper and Case 1992b). We are aware of only one exception: Taper and Case (1985) analyzed a more

realistic quantitative genetic model where specialization (called "within-phenotype niche width" in their article) could evolve as well. This latter study, however, did not address the question whether increased specialization may allow invasion of additional species.

Third, and most importantly, earlier models of character displacement did not take foraging behavior into account. To our knowledge, the exceptions are Brew (1982, 1984), who studied character displacement in a purely ecological setting, with a fixed number of species and without the evolution of specialization. Therefore, the study presented here would appear to be the first to investigate the effects of foraging behavior on the combined evolution of character displacement and resource specialization. In our model, the number of herbivore phenotypes, their level of specialization, and the amount of character displacement among them are dynamically determined by the outcome of herbivore evolution, which in turn is driven by a reasonably realistic feedback involving the underlying population dynamics and behavioral dynamics (Fig. 1).

MODEL DESCRIPTION

In this section, we use standard descriptions of consumer-resource dynamics to formulate a model that is widely applicable to herbivore-plant systems and particularly to herbivorous arthropods and their host plants. In the Discussion we reflect on how alternative model assumptions may affect the results.

Plant Quality

We consider plant types arranged along a quality gradient. The word "quality" is used here in a very specific sense: it reflects the ultimate potential for per capita growth of the herbivore. This notion is inspired by the observation from insect-plant biology that plants harbor intrinsic differences

that are relevant for herbivores, irrespective of how well the arthropod in question is adapted to one plant species or the other. Such differences affect both the intrinsic growth rate and the carrying capacity of herbivores.

To highlight the relevance of such measures of quality in nature, we provide two examples. First, assume that plant quality is primarily determined by one limiting nutrient. Nitrogen content, for instance, has been recognized for years as a critical factor limiting herbivore growth (Slansky and Feeny 1977; McNeill and Southwood 1978; Mattson 1980; Denno and McClure 1983; Strong et al. 1984; White 1993; Fagan et al. 2002). Then, plant types can be ranked according to nitrogen content as a relevant measure of quality. Second, assume that plant quality is primarily determined by a measure of toxin content. The distribution of major secondary metabolites that function in plant defense is almost mutually exclusive among plant families (e.g., Wink 2003). Thus, plant types within one family produce similar secondary metabolites and can be placed along a continuum from low to high quality. Of course, the relevant measure of plant quality can also be a combination of toxin and nutrient content. Correlations between such measures arise because plants with higher nutrient content are subject to selection for increased defense (Herms and Mattson 1992).

Plant Population Dynamics

In our model, the density $p(q)$ of plants with quality q follows standard Lotka-Volterra dynamics,

$$\frac{d}{dt}p(q) = r(q)p(q) \left[1 - \frac{p(q)}{K(q)} \right] - c_f h u(q) p(q), \quad (1)$$

where $r(q)$ and $K(q)$ are, respectively, the intrinsic growth rate and carrying capacity of plants with quality q ; c_f is the feeding rate per plant per herbivore; h is the number of herbivores; and u is the herbivores' resource utilization spectrum, describing their proportional utilization of plant qualities (see Foraging Behavior). The dynamics in equation (1) thus describe changes in the herbivores' resource availability spectrum $p(q)$.

Feeding Efficiency

Feeding efficiency describes how well a herbivore can digest a specific plant quality. Because the quality of plants is determined by a diversity of toxins and/or nutrients and feeding efficiency depends on a large number of underlying physiological traits, high feeding efficiency on toxins and/or nutrients of a plant with one quality does not necessarily imply high feeding efficiency on the (different) toxins and/or nutrients of a plant with another quality. Accordingly, herbivores face a trade-off in feeding efficiency when exploiting different plant qualities. They can either specialize by becoming highly efficient on relatively narrow intervals of the plant quality gradient or forego such high efficiency and instead adjust their physiology in a generalist manner to achieve intermediate feeding efficiency across all plant qualities. This trade-off is modeled by assuming a normal distribution of feeding efficiency along the plant quality gradient,

$$e(q) = \exp \left[-\frac{1}{2}(\mu - q)^2/\sigma^2 \right] / (\sqrt{2\pi}\sigma). \quad (2)$$

The mean μ of the efficiency spectrum $e(q)$ determines the focal range of plant qualities utilized by a herbivore, while the standard deviation σ defines the herbivore's niche width and thus determines its level of specialization (for a review of empirical data, see Kassen 2002). A low value of σ implies a relatively high efficiency in a narrow range of the plant quality gradient, whereas a high value results in a relatively low efficiency, yet in a wide range. We study the joint evolution of the adaptive traits μ and σ .

Foraging Behavior

We assume that behavior underlying habitat choice is driven by maximization of food intake and that changes in foraging behavior occur on a fast time scale relative to population dynamics. Optimally foraging herbivores will redistribute as soon as their feeding has decreased the density of the currently most attractive plant quality to an extent that plants of different quality yield more. Therefore, the distribution of herbivores over the plant gradient can change continuously over time (Krivan 1997). The gain $g(q)$ that an individual herbivore can extract from plants of quality q is defined as its intake rate when feeding on those plants exclusively. This is a product of plant quality q , feeding rate c_f , plant biomass $p(q)$, and feeding efficiency $e(q)$, which depends on μ and σ , as described in equation (2),

$$g(q) = qc_f p(q) e(q). \quad (3)$$

This gain function $g(q)$ describes a herbivore's intake rate from feeding on plants of quality q and determines its per capita growth rate, as will be specified in detail below (see Herbivore Population Dynamics). Therefore, $g(q)$ is an appropriate measure for herbivores to decide which plants to feed on.

Foraging behavior is generally subject to error, preventing individuals from foraging optimally. Such errors may result from various causes, such as the need of individuals to sample their environment before being able to make a decision or from constraints on the sensory perception and mobility of foragers. In our model, suboptimal levels of foraging are described phenomenologically by means of a flexible power law, so that the utilization $u(q)$ of plants with quality q is proportional to $g(q)^\alpha$,

$$u(q) = C(\sigma) \frac{g(q)^\alpha}{\int g(q)^\alpha dq}. \quad (4)$$

The denominator above is only needed to ensure proper normalization of the probability distribution u . The factor $C(\sigma)$ reflects the fact that specialists need more time to search for the specific plants they are specialized on and therefore can spend less time exploiting those plants. We describe this phenomenologically by $C(\sigma) = \sigma/(\sigma + c_s)$, where the half-saturation constant c_s measures the cost of specialization.

The parameter α can take any value in the range $(0, +\infty)$ and provides a conveniently flexible way of describing a herbivore's foraging accuracy. Setting α to zero yields non-

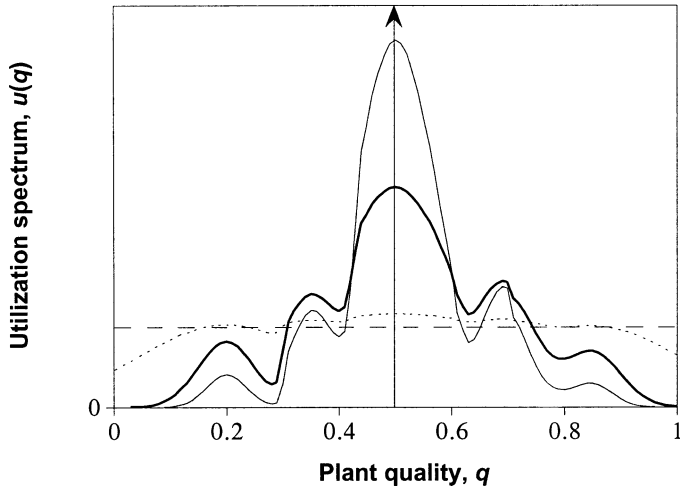


FIG. 2. Utilization spectra along the plant quality gradient, for a hypothetical gain function (proportional to the thick solid curve) and different values of the foraging accuracy parameter α . The distribution for $\alpha = 1$ is simply proportional to the gain distribution (thick continuous curve). The other distributions shown are for $\alpha = 0$ (dashed curve; nonselective foraging: herbivores use all existing plant qualities with equal probability), $\alpha = 0.1$ (dotted curve), $\alpha = 2$ (thin continuous curve), and $\alpha \rightarrow \infty$ (vertical arrow; optimal foraging: herbivores use only the plant quality yielding the highest gain).

selective feeding (utilization is uniform and completely independent of gain), whereas letting α go to infinity yields dynamic optimal foraging (utilization is strictly limited to resources offering maximal gain). Values of α in between these two extremes result in selective, but suboptimal foraging (Fig. 2). For example, when $\alpha = 1$, the utilization $u(q)$ of plants with quality q is proportional to the gain $g(q)$ from those plants. We do not consider evolutionary change in α , because foraging errors act as evolutionary constraints that naturally result from sampling the environment and from limitations in sensory perception and mobility.

Herbivore Population Dynamics

The per capita birth and death rates of herbivores are functions of their intake rate, I . The latter is the product of gain and utilization, integrated over the gradient of plant qualities,

$$I = \int g(q)u(q) dq. \quad (5)$$

Individuals can produce offspring if their intake rate exceeds a threshold I_{\min} . Above this threshold, the birth rate $b(I)$ is a saturating function of intake (Fig. 3). The death rate $d(I)$ is asymptotically declining from the starvation mortality d_{\max} toward a background mortality d_{\min} (Fig. 3). In the model, we used the functions $b(I) = b_{\max}\{1 - \exp[-c_b(I_{\min} - I)]\}_+$ and $d(I) = d_{\min} + (d_{\max} - d_{\min})\exp[-c_d I]$. Here, b_{\max} is the maximum birth rate, and c_b is a scaling constant determining the slope of increase. The function $(\cdot)_+$ maps any negative values to zero. For the mortality rate, c_d is a scaling constant determining the slope of decrease. A herbivore's per capita

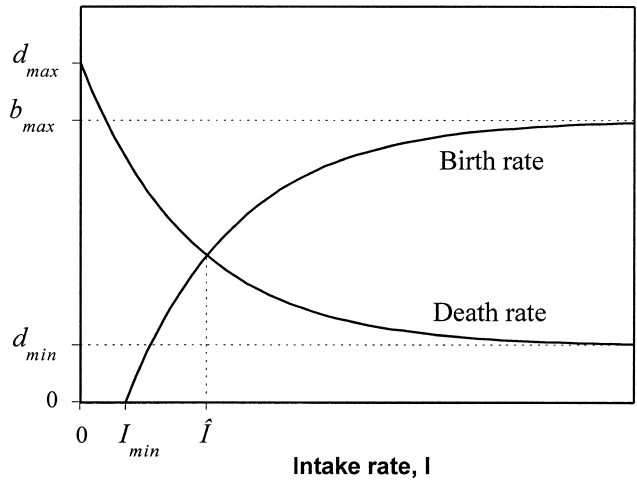


FIG. 3. Birth and death rates as functions of intake rate. Herbivores can produce offspring if their intake rate exceeds a threshold I_{\min} . Above this threshold, the birth rate $b(I)$ is a saturating function of intake. The death rate $d(I)$ is asymptotically declining from the starvation mortality d_{\max} toward a background mortality d_{\min} . Growth rate is zero for an intake rate \hat{I} that satisfies $b(\hat{I}) = d(\hat{I})$.

growth rate is $b(I) - d(I)$, so that the number of herbivores, h , changes according to

$$\frac{d}{dt}h = [b(I) - d(I)]h. \quad (6)$$

Note that the intake rate \hat{I} at population dynamical equilibrium satisfies $b(\hat{I}) = d(\hat{I})$.

Evolutionary Dynamics

The herbivore's fitness landscape is determined by the invasion fitness of rare phenotypes, defined as the long-term per capita growth rate of such phenotypes in the environment determined by the resident population at its population dynamical equilibrium. The expected rate of deterministic phenotypic evolution is then proportional to the local fitness gradient. An individual-based version of the model is used to investigate higher degrees of polymorphism; this also allows checking the robustness of conclusions obtained from the deterministic model (see Appendix 1 for a full description).

RESULTS

We first examine two extreme cases: nonselective foraging and optimal foraging, the latter of which is shown to yield unrealistic evolutionary outcomes. Because optimal foraging is also biologically unrealistic, the remainder of this section focuses on suboptimal foraging.

Nonselective Foraging: $\alpha = 0$

In general, the equilibrium of the plant-herbivore population dynamics cannot be derived analytically, and this therefore also applies to the invasion fitness of herbivores. However, for nonselective foraging, we can show that all equilibrium plant densities $\hat{p}(q)$ are negatively correlated with

\hat{h} , the equilibrium number of herbivores (see Appendix 2). A mutant herbivore that can invade a population of resident herbivores, must decrease the plant densities to lower levels than $\hat{p}(q)$ in order to grow, causing the resident type to decline in density. Consequently, the mutant can invade the resident population if and only if it decreases plant densities to lower levels than $\hat{p}(q)$, and thereby grows to a higher equilibrium \hat{h} . This implies that an optimization principle (Mylius and Diekmann 1995; Metz et al. 1996b) exists under nonselective foraging: herbivore evolution then leads to a strategy (μ, σ) that maximizes the equilibrium number of herbivores by minimizing the equilibrium density of plants. An optimal strategy in such a scenario possesses three important features (Meszena et al. 2001): it is evolutionarily singular (selection pressures vanish at the optimal strategy), it is convergence stable (gradual evolution converges on the optimal strategy), and it is evolutionarily stable (no other strategy can invade the evolving population once the optimal strategy has been attained). Such a strategy is referred to as a continuously stable strategy (CSS; Eshel 1983).

Which exploitation strategy will be optimal under nonselective foraging? Notice that under nonselective foraging plant densities at population dynamical equilibrium are proportional to their carrying capacities, making the herbivore's intake \hat{I} is proportional to $C(\sigma) \int qK(q)e(q) dq$ (see Appendix 2). This function is maximized when the mean μ of $e(q)$ is at the maximum of $qK(q)$. The standard deviation σ of $e(q)$ for which intake is maximized depends on the specialization cost c_s ; σ increases from zero when c_s increases from zero. Simulations tracking the evolutionary dynamics in the strategy (μ, σ) confirm these results. Under nonselective foraging, therefore, it always pays to specialize on the plant quality offering the best compromise between quality q and abundance K , even though nonselective herbivores cannot avoid using the entire gradient of plant qualities.

Optimal Foraging: $\alpha \rightarrow \infty$

To understand the population dynamics under optimal foraging, consider the situation in which all plant types are at their carrying capacity and a herbivore phenotype with strategy (μ, σ) and enters the system. (We assume throughout this section that optimal foragers cannot have a foraging cost of specialization, $c_s = 0$.) Typically, a single plant quality will offer the highest gain to this herbivore. The herbivores will start depleting that plant quality (and, because of optimal foraging, only that quality), thereby decreasing its gain. At some point, adjacent plant qualities will yield gains equal to the initially exploited one, and thus the herbivores will start using the corresponding range of plant qualities uniformly. This process will continue until the herbivores reach their population dynamical equilibrium. Here, the gain distribution over the quality gradient will resemble a table mountain. All plant qualities used will yield equal gain (given by \hat{I} ; see Appendix 3), and the herbivores' utilization spectrum will be rectangular, implying equal utilization of all plant qualities used. Plant qualities with a gain below \hat{I} are not used at all by the optimally foraging herbivores, and therefore their equilibrium densities remain at carrying capacity.

Again, the population dynamical equilibrium and thus the

resultant invasion fitness cannot be derived analytically. We can conclude, however, that under optimal foraging no evolutionarily singular strategy exists: any monomorphic population of resident herbivores can always be invaded by any mutant of small effect, because such mutants have a higher efficiency for at least one specific plant quality that is in use by the resident population. These plant qualities then yield a gain higher than \hat{I} (because they yield a gain equal to \hat{I} for the resident individuals), and, as the new phenotype forages optimally, it starts using these plant qualities exclusively and thus attains a positive growth rate (see Appendix 3).

For polymorphic herbivore populations an analogous line of reasoning applies: any new herbivore phenotype can invade if its efficiency function yields a gain higher than \hat{I} on any of the plant qualities. This conclusion changes as soon as all plant qualities are utilized by the herbivores. Then, herbivores with efficiency functions broadened relative to that of residents cannot invade any more, because they find the plant quality for which their gain is highest exploited to a level lower than \hat{I} . By contrast, more specialized herbivores can always invade a more generalist niche-sharer (i.e., a phenotype with a larger value of σ , but the same value of μ ; see Appendix 3). Therefore, evolution under optimal foraging leads to a theoretically infinite diversity of extreme specialists (each with a population density approaching zero) at all plant qualities q at which plant density is high enough to sustain such specialists.

Suboptimal Foraging: Deterministic Approximation

Herbivore evolution under suboptimal foraging ($0 < \alpha < \infty$) is analyzed numerically. For the sake of brevity, we describe the evolutionary dynamics for $\alpha = 1$ (i.e., with utilization proportional to gain) and $c_s = 0$ (i.e., without a cost of specialization). Appendix 4 shows that this case is representative for a wide range of α values and for specialization costs that are not too high.

Starting out with a single herbivore strategy, gradual evolution of herbivore phenotypes leads to a globally attractive singular strategy (Fig. 4a), where the herbivores homogeneously utilize almost the entire resource gradient (Fig. 4b), creating a gain curve much like the table mountain of optimal foragers. This singular strategy is an evolutionary branching point: when the fitness gradient for both μ and σ has declined to zero, mutants of small effect can still invade the resident population (in contrast to the case of a CSS; Geritz et al. 1998). The resultant disruptive selection can cause the population to become dimorphic.

During such evolutionary branching, one herbivore phenotype initially specializes on higher-quality plants, while the other becomes more generalist and focuses on lower-quality plants (Fig. 5a). This divergence arises because low-quality plants are underexploited at the branching point. Therefore, herbivores can do better either by specializing on higher-quality plants or by becoming generalists on lower-quality plants.

While the two phenotypes diverge in trait space, their mutual impact through the feedback on plant densities declines. To quantify this, two characteristics are useful: the intersection point q^* of the utilization spectra of the two phenotypes

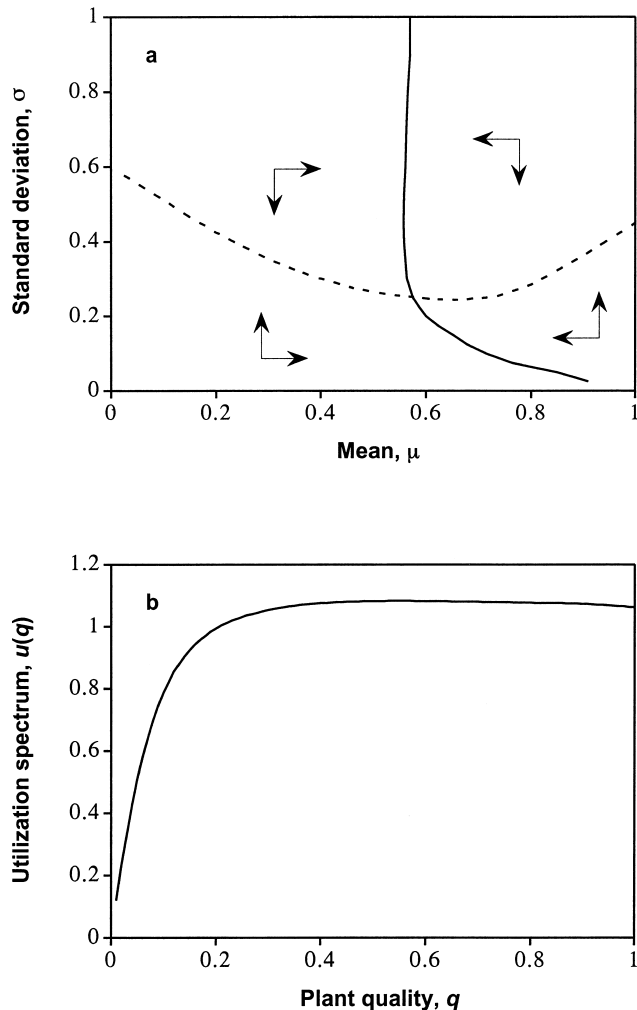


FIG. 4. Monomorphic evolution of the herbivores' efficiency strategy (μ , σ) in a population with suboptimal foraging. (a) Evolutionary phase portrait, showing two isoclines and the directions of evolutionary change in between. The continuous curve is the evolutionary isocline for the mean μ , and the dashed curve is the isocline for the standard deviation σ . The evolutionarily singular strategy, where both isoclines cross, is an evolutionary branching point. (b) Utilization spectrum along the plant gradient at population dynamical equilibrium, as determined by the singular strategy in (a). Parameters: $K(q) = 50 + 10 \cdot N_{0.1}(q - 0.5)$, $r(q) = 1$, $b_{\max} = 1.0$, $c_f = 0.0025$, $c_b = 400$, $c_d = 1200$, $c_s = 0$, $d_{\max} = 1.0$, $d_{\min} = 0.02$, $I_{\min} = 0.0005$, and $\alpha = 1.0$.

and their total overlap Δu . The intersection point q^* describes the plant quality along the resource axis at which the two phenotypes exhibit equal utilization; it can be interpreted as the border between their foraging ranges. By contrast, the total utilization overlap Δu (i.e., the roughly triangular areas in Figs. 5d–f, peaked at q^*) measures the amount of competition between the two phenotypes. Plotting q^* and Δu against each other reveals two distinct phases in the coevolutionary process (Fig. 5b).

In the first, character-displacement phase, competition drives the two phenotypes apart: the total utilization overlap quickly declines, while the intersection point shifts toward higher qualities. This is a fast process, indicating large fitness

benefits for avoiding competition. The two phenotypes evolve strategies that lead them to forage on distinctly different plant quality ranges (cf. Figs. 5d, e). During this phase, the lower-quality phenotype increases in abundance by exploiting an increasingly wider range of the plant gradient, while the number of individuals in the higher-quality phenotype declines by specializing on a small but high-quality range of the plant gradient (Fig. 5c). At the end of this phase, total utilization overlap is minimized (Fig. 5e), and with it the strength of competition between the two phenotypes (Fig. 5b).

In the second, coevolutionary niche shift-phase, the higher-quality phenotype still experiences selection for specialization: generalists cannot invade into its population, as the resident phenotype already uses the entire range of resources between the high-quality border of the plant gradient and the range dominated by the lower-quality phenotype. This reduces the realized niche width of the higher-quality phenotype, which, in turn, gives evolutionary opportunity for the lower-quality phenotype to expand its niche width. Hence, the intersection point progresses slowly but steadily toward higher plant qualities, whereas the total utilization overlap essentially remains constant (Fig. 5b). This process causes the evolutionary trajectory of the lower-quality phenotype to change direction (Fig. 5a).

The coevolutionary process ends up at a pair of strategies, with the lower-quality phenotype being more generalized and the higher-quality type more specialized (Fig. 5a). Their utilization spectra come close to the rectangular shapes of optimal foragers (Fig. 5f). These two singular strategies are again evolutionary branching points, so that subsequent evolutionary change can lead to trimorphic and quadrimorphic herbivore populations.

Suboptimal Foraging: Individual-based Model

Analyzing the continued evolutionary dynamics becomes tedious using the deterministic approximation—using an individual-based model is then more efficient (see Appendix 1 for details). Evolution in the individual-based model resembles adaptive radiation in the μ -dimension, leading to many specialized types (Fig. 6). However, in contrast to the deterministic approach, the coevolutionary niche-shift phase is generally absent: typically, a new split already occurs before this phase sets in. This is because mutational steps are finite and reproduction is asexual in the individual-based model. While weak directional selection would still be expected to drive the coevolutionary niche-shift phase, herbivores are already so close to the fitness minimum that even small mutational steps suffice to jump across this fitness minimum, thus initiating a split that would not yet have occurred if mutational steps were infinitely small or if speciation is slow. Specifically, a sexual population is expected to linger much longer at a fitness minimum before, if ever, disruptive selection can cause reproductive isolation. Sexual herbivores must thus be expected to display both coevolutionary phases as characterized above.

The resulting community of specialists eventually becomes impervious to further invasion by any herbivore phenotype. On the one hand, more generalist herbivores, even though they can use a wider range of the gradient, are outcompeted

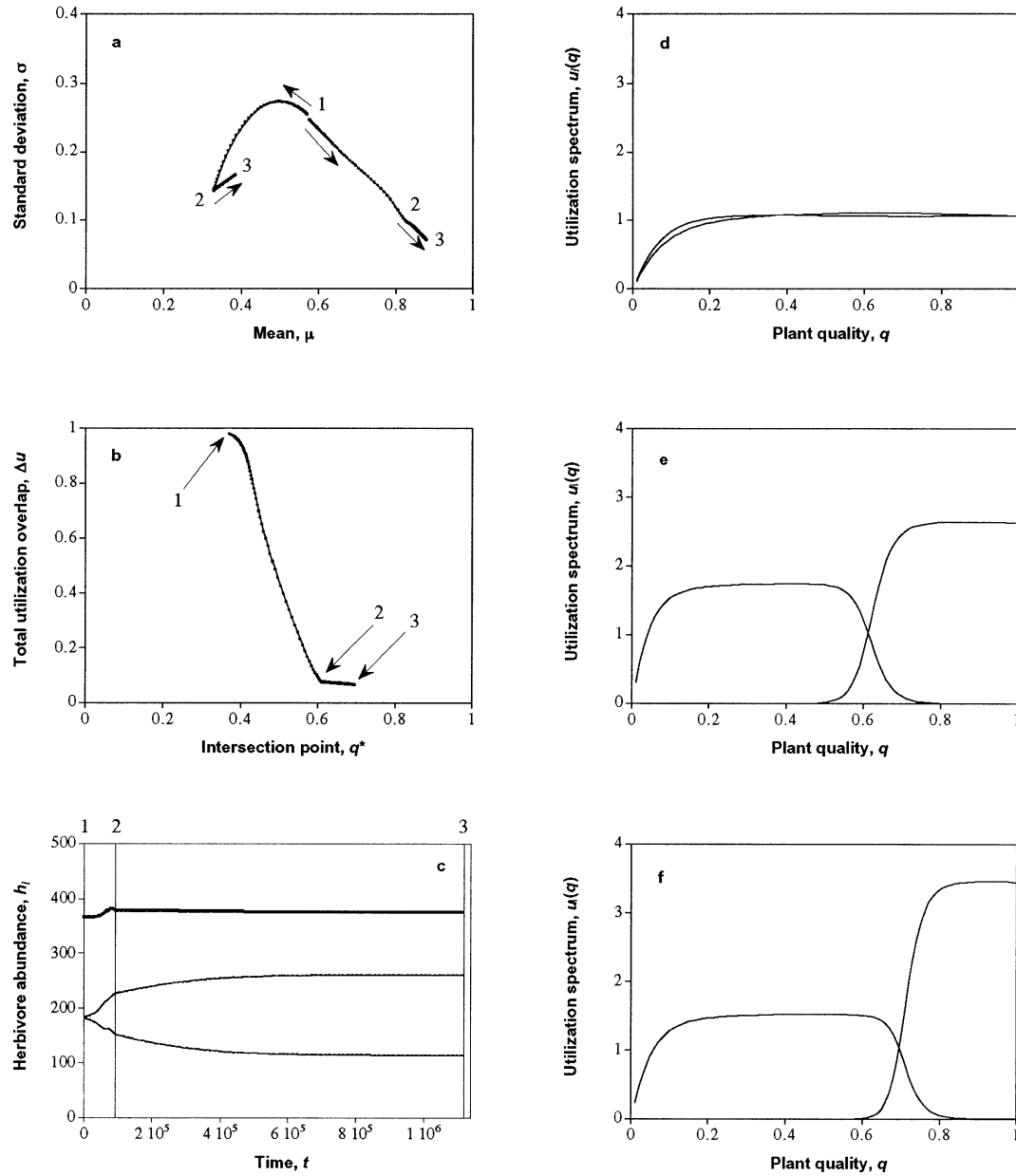


FIG. 5. Dimorphic evolution of the herbivores' efficiency strategy. (a) Evolutionary trajectories of the two phenotypes. Starting from the primary evolutionary branching point (Fig. 4a), subsequent evolutionary change proceeds as indicated by the arrows. Positions 1, 2, and 3 in (a–c) correspond to the starting point, turning point, and end point of dimorphic evolution, respectively. Utilization spectra from positions 1, 2, and 3 are presented in (d–f), respectively. (b) Covariation of total utilization overlap between the two phenotypes (Δu) and of the intersection point of their utilization spectra (q^*). The first, fast phase of evolutionary change features ecological character displacement, strongly reducing the utilization overlap, whereas the second, slow phase is characterized by coevolutionary niche shift: the intersection point shifts to higher plant qualities, while the total utilization overlap remains essentially constant. (c) Resultant changes in herbivore abundances (thin curves; the herbivore morph specializing on low plant qualities has the higher densities). Total herbivore abundance is shown by the thick curve and increases until the end of the character displacement phase (position 2). (d) Initial utilization spectra of the two phenotypes in the population, corresponding to position 1 in (a–c). (e) Utilization spectra of the two phenotypes at the end of the character displacement phase, corresponding to positions 2 in (a–c). (f) Utilization spectra of the two phenotypes at the dimorphic evolutionary attractor, corresponding to positions 3 in (a–c). Parameters as in Figure 4.

everywhere by the specialized herbivores already present. On the other hand, more specialized herbivores have to pay a larger cost of specialization, causing them to lose the competition against the resident specialists. Because of this global evolutionary stability, it does not matter how the evolutionary

game is started. To confirm this, we considered a variation of our model in which 1% of the mutants are chosen at random from the full range of phenotypes, instead of resembling their parents. Widely different herbivore phenotypes are then quickly established; yet the resultant evolutionary outcome

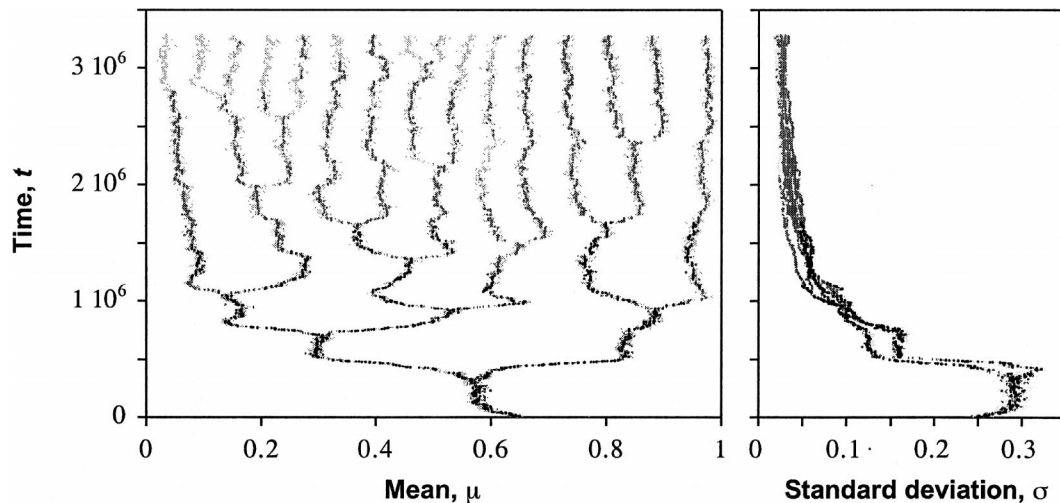


FIG. 6. Polymorphic evolution of the herbivore's efficiency strategy in the individual-based model. The left panel shows the evolution of a diversity of phenotypes along the plant quality gradient (black branches consist of more than 200 individuals, dark gray branches of 100–200 individuals, and light gray branches of less than 100 individuals). The right panel shows the concomitant changes in the standard deviation σ of the herbivores' efficiency spectra. Specialization sharply increases as the number of branches increases. Parameters as in Figure 4; except $s_m = 0.005$, $p_m = 0.0003$, $r(q) = 3$, and $c_s = 0.1$.

is indistinguishable from a community built up through gradual evolution by small mutational steps.

Not surprisingly, the number of specialists in the resulting community decreases when the cost of specialization is increased. However, the degree of ecological character displacement among the specialists is not affected by this cost (see Appendix 4, Fig. A3).

DISCUSSION

We have shown that, along a gradient of plant quality, frequency-dependent selection emerging from competition under suboptimal foraging can lead to the buildup of a community of increasingly specialized herbivore phenotypes (Figs. 5, 6). Such diversification (reminiscent of adaptive radiation; Schluter 2000a,b) follows a characteristic evolutionary pattern and occurs for a wide range of specialization costs and of foraging accuracies. Because of this broad robustness, our findings are likely to be applicable to a variety of consumers other than herbivores.

Alternative Assumptions

To what extent do the results reported here depend on underlying assumptions? For reasons of tractability, our individual-based model neglects sexual reproduction. By contrast, the deterministic approximation of evolutionary dynamics, in which the rate of evolutionary change is proportional to the local fitness gradient, applies to sexual models (Lande 1979) just as well as to asexual models (Dieckmann and Law 1996). In general, a distinction between sexual and asexual evolution is not critical as long as genetics are additive and mutations do not have too large an effect (e.g., Taylor 1989; Charlesworth 1990; Christiansen 1991; Iwasa et al. 1991; Taper and Case 1992a; Abrams et al. 1993b; Weissing 1996; Van Dooren 2004) and frequency-dependent selection does not favor evolutionary branching (e.g., Dieck-

mann and Doebeli 1999; Abrams 2001; Van Dooren 2004). It must be noted, however, that recombination promoting sufficient cohesion of a sexual population's gene pool (e.g., Felsenstein 1981; Dieckmann and Doebeli 1999) is expected to delay or even prevent some of the branching events (Fig. 6). Interestingly, such delays underscore the importance of the two characteristic coevolutionary phases identified in this study (see below).

A second set of critical assumptions relates to preventing unstable population dynamics by assuming a linear functional response and logistic plant growth. Alternative assumptions resulting in equally stable population dynamics (e.g., saturating functional response and semichemostat plant growth) will not affect the results qualitatively. If, however, the potential for unstable dynamics is incorporated, increasing herbivore specialization may lead to population dynamical destabilization. The resulting degree of specialization may then be lower, because generalists can cope better with resource fluctuations (Slatkin and Lande 1976; Rosenzweig 1987; Brown 1989; Wilson and Yoshimura 1994). This particular ecological feedback into the evolutionary process of specialization deserves additional research.

Finally, the assumption of a linear trade-off in feeding efficiency $e(q)$ does not appear to be critical. Nonlinear trade-offs (implying that $\int e(q) dq$ decreases or increases with σ , resulting in so-called weak and strong trade-offs, respectively) can be viewed as imposing an alternative cost of specialization/generalization. Strong trade-offs are expected to lead to even more specialization, but weak trade-offs might favor generalists (and therefore prevent evolutionary branching), especially when foraging is not or only weakly density dependent. However, simulations (not shown here) indicate that weaker trade-offs do not generally seem to select for generalists, even under conditions of very suboptimal foraging ($\alpha < 1$). This makes sense, because the intake rate of herbivores is unaffected when the cost of specialization is

applied to efficiency e (affecting gain g) instead of utilization u (see eq. 5).

The Interplay between Ecological Character Displacement and Specialization

By assuming a gradient of resources, we studied the joint evolution of the focal point as well as the range of resource utilization. In this way, we explicitly analyzed the joint evolution of specialization and ecological character displacement. Most earlier models of character displacement studied evolution of distance between niches along a resource gradient, but kept the niche width constant (see the review by Taper and Case 1992b; for a model in which specialization, called “within-phenotype niche width,” could evolve as well see also Taper and Case 1985). Interestingly, evolution of specialization and ecological character displacement have not often been brought into contact before, possibly because character displacement studies usually deal with evolution of the range of resources used and not with evolution of the efficiency of resource utilization.

Key insights from our model, therefore, arise from the interplay between the evolutionary processes of specialization and character displacement. First, the primary evolutionary branching in the herbivore population always results in a specialist utilizing heavily exploited plants of high quality and a generalist utilizing plant qualities that are less extensively used. Whenever the underlying resource gradient is asymmetric, the likelihood of the initial divergence being completely neutral in σ is negligible. In any such consumer-resource model, combining character displacement with specialization evolution, we must therefore expect the displacement to result in one consumer species initially becoming more generalist. Clearly, at short evolutionary time scales Simpson’s (1953; see also Schluter 2000a) empirical view that specialists descend from generalist ancestors in an adaptive radiation does not hold. However, given a long enough evolutionary time scale, our model is in agreement with Simpson’s observation (Fig. 6).

A second important aspect of the interplay between specialization and character displacement is the prediction of two characteristic phases in the divergence of a species pair: a fast character-displacement phase, during which overlap in the plant utilization of herbivore species is minimized, is typically followed by a slow coevolutionary niche-shift phase, during which herbivore species jointly adjust their niches leading to maximized overall plant utilization. In addition, this two-phase pattern of consumer coevolution is likely to apply to other consumer-resource systems.

Limiting Similarity and the Evolution of Specialization

We have shown that optimal foraging ($\alpha \rightarrow \infty$) in our model would lead to an unrealistic, infinite diversity of extreme specialists, each exploiting an infinitely narrow part of the plant gradient (reminiscent of a conjecture by Vincent et al. [1993] for Lotka-Volterra models in which the resource gradient was unbounded and the competitive effects among species were smaller than those within species). In this case, limiting similarity between the phenotypes would approach zero, and species packing along the plant gradient would be

infinitely dense. In their original study on limiting similarity, MacArthur and Levins (1967) proved that rectangular utilization curves allow for infinite species packing, but a biological interpretation was not given. Here we have shown that these curves apply to consumers capable of dynamical optimal foraging.

In the strict sense, optimal foraging is a biologically unrealistic assumption, because it requires omniscience and unlimited mobility. Real foragers need to sample their environment: herbivorous arthropods need time to select their host plant, exhibit stagedependent mobility, and mothers may not always select the best host for their (immobile) offspring (e.g., Wainhouse and Howell 1983; Rauscher 1983; Rauscher and Papaj 1983; Whitham 1983; Robertson 1987; Moran and Whitham 1990; Valladares and Lawton 1991; Underwood 1994). Evidence is accumulating that they can approximate optimal foraging by adaptive learning (Dukas and Bernays 2000; Egas and Sabelis 2001; Egas et al. 2003; Nomikou et al. 2003). Our model incorporates such behavior as suboptimal foraging.

We have shown that suboptimal foraging ($0 < \alpha < \infty$) limits the number of specialist herbivores evolving. Due to suboptimal foraging, the range of plant qualities a herbivore species exploits always exceeds the range on which it is specialized, thereby leaving less opportunity for other specialists to invade. Consequently, the number of specialist herbivores decreases with the foraging accuracy α (Appendix 4). Adding a cost of specialization to the foraging behavior also limits the number of phenotypes, by limiting their levels of specialization (Appendix 4). In line with our findings, Mitchell (2000) showed a similar limit to species richness along a gradient as a consequence of increasing travel costs. He also noted the possibility of evolutionary branching (using the term “evolutionarily stable minima”).

Nonselective foraging of the herbivores ($\alpha = 0$) in our model leads to a single CSS, instead of a polymorphism. Therefore, limiting similarity does not apply. The herbivore CSS is, in terms of the physiological definition we use in this paper, a specialist strategy, even though it cannot help but utilize the entire gradient of plant qualities (and hence remains a generalist when defined in terms of foraging behavior).

Ecological Character Displacement

The degree of ecological character displacement in the evolutionarily stable community depends on the level of suboptimal foraging, but not on the cost of specialization (Appendix 4). The better a herbivore is able to home in on plants with higher gains, the better it can keep its realized niche separate from its competitors. Consequently, the degree of ecological character displacement, based on the evolved fundamental niche characteristics (μ and σ), will be lower for more discriminate foragers. The cost of specialization does not influence character displacement because it does not affect the ability of herbivores to minimize competition with other herbivores by foraging on disjunct ranges of the plant gradient.

An important factor affecting ecological character displacement in previously studied models is the shape of the

carrying capacity distribution (MacArthur and Levins 1967; Slatkin 1980; Taper and Case 1985; Drossel and McKane 1999, 2000). Character displacement is favored when this distribution is uniform (not dropping off toward the edges, as a Gaussian distribution does). For such uniform distributions, phenotypes diverging in trait space incur no fitness cost that may outweigh the benefits of reduced competition. Because we took foraging behavior into account, we need to consider the shape of the gain curve g rather than that of the carrying capacity K . Any selective foraging behavior flattens the gain curve, and hence favors character displacement—irrespective of the shape of K .

A fundamental open question is whether a single quality axis can approximately describe how herbivorous arthropods experience plant types. In general, the growth rate of herbivorous insects appears to be limited by nutrients, rather than by energy (Schoonhoven et al. 1998, ch. 4). Usually, one axis for proteins and one for carbohydrates will capture most variation in growth rate (Simpson and Raubenheimer 1996; Raubenheimer and Simpson 1999). However, other axes may be important, for example, due to the presence of secondary plant metabolites (increasing toxicity or decreasing digestibility). The general effects of increasing the dimension of trait spaces on the properties of evolutionary branching points are still largely unknown. Yet, we propose that adding more quality dimensions will increase, rather than decrease, the possibilities for frequency-dependent selection to induce adaptive radiation (see also Yoshiyama and Roughgarden 1977; Pacala and Roughgarden 1982), simply because a multiplicity of trait dimensions provides more opportunity for specialization and ecological character displacement.

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APPENDIX 1: ADAPTIVE DYNAMICS

The theory of adaptive dynamics describes evolutionary processes in asexual populations under frequency-dependent selection, explicitly incorporating the inherently stochastic nature of these processes and offering techniques for simplifying their analysis (Metz et al. 1992, 1996; Dieckmann 1994; Dieckmann and Law 1996; Dieckmann 1997; Geritz et al. 1997, 1998). Individual-based models, including both demographic and mutational stochasticity, are the natural starting point for such a framework. Such models, however, are very time-consuming and often cumbersome and inconclusive to study. Therefore, in addition to using individual-based models, we base our investigation on a deterministic approximation, the canonical equation of adaptive dynamics. In this systematically derived approximation, the dynamics of resident populations are treated deterministically and the evolutionary change that arises from small mutational steps expressed by successful invaders deterministically follows the local gradient of the fitness landscape around a resident phenotype. Assuming that in long-term asexual evolution relevant mutations occur at low probability (mutation-limited evolution), adaptation can be studied by evaluating the fate of mutants in populations that consist of one or more resident phenotypes at their ecological equilibrium (here we use the term “ecological equilibrium” to describe the joint outcome of behavioral dynamics and population dynamics).

More specifically, the fitness landscape of adaptive dynamics is determined by the invasion fitness of mutant phenotypes, defined as the long-term per capita growth rate of a rare mutant in the environment set by the resident population at its ecological equilibrium (Metz et al. 1992). A resident phenotype can be invaded and ousted by mutant phenotypes with positive invasion fitness. Accounting for the demographic stochasticity of such advantageous mutants, the resultant rate of phenotypic change is proportional to the local fitness gradient (Dieckmann and Law 1996), in line with analogous findings for models based on quantitative genetics (Lande 1979; see also Abrams 2001).

When the adaptive dynamics eventually reach a phenotype at which the fitness gradient vanishes, it has attained a so-called evolutionarily singular strategy (ESS). Singular strategies can be of several types (Dieckmann 1997; Geritz et al. 1997, 1998; see also Christiansen 1991), two of which are encountered in this study: continuously stable strategies and evolutionary branching points. A continuously stable strategy (CSS; Eshel 1983) is a strategy that is an evolutionary attractor (i.e., a singular strategy that is convergence stable) and that also cannot be invaded by any neighboring phenotype (i.e., the singular strategy is locally evolutionarily stable). Note that an ESS differs from a CSS in that the former does not require the first condition to be satisfied (i.e., an ESS is not necessarily an evolutionary attractor; Eshel and Motro 1981). By contrast, an evolutionary branching point is an evolutionary attractor that is not evolutionarily stable (Metz et al. 1992, 1996; Geritz et al. 1998). Mutants close to such a singular strategy have a chance to mutually invade each other and form a stable dimorphism. The resulting dimorphic adaptive dynamics allow for two resident phenotypes and describe the initial phenotypic divergence and subsequent evolutionary change in the two subpopulations. Such a pair is again expected to converge to a singular strategy, the evolutionary stability of which can once more be determined by evaluating whether mutants of small effect around the singular strategy are able to invade.

Although the deterministic approximation is a versatile tool for investigating the adaptive dynamics under low degrees of polymorphism (monomorphic and dimorphic evolution), it becomes a bit tedious thereafter. An individual-based model, by contrast, is naturally suited to investigating adaptive dynamics involving multiple evolutionary branching events. Therefore we use an individual-based version of the deterministic model to investigate higher degrees of polymorphism. At the same time this model allows checking the robustness of evolutionary conclusions obtained from the deterministic approximation when relaxing the simplifying assumptions that approximation is based on (e.g., mutation-limited evolution and small mutational steps).

In the individual-based model, all individual herbivores can be assigned different phenotypes (μ , σ), and demography as well as mutations are treated stochastically. Based on herbivore birth and death rates from the deterministic equations, the waiting times for the next birth or death event to take place are drawn from an exponential probability distribution (Gillespie 1976; Van Kampen 1981; Dieckmann 1994; Dieckmann et al. 1995). During a birth event, the phenotype of offspring individuals can either be faithfully inherited from their parent or it can be affected by mutation. The latter occurs with probability p_m , and the mutant phenotype is then drawn from a normal distribution with standard deviation s_m around the parental phenotype.

APPENDIX 2: NONSELECTIVE FORAGING: ($\alpha = 0$)

Under nonselective foraging, herbivore utilization is uniformly distributed over the plant quality gradient: the utilization spectrum $u(q)$ is flat. Because total utilization must equal $C(\sigma)$ (see eq. 4), the utilization spectrum is then given by

$$u(q) = \frac{C(\sigma)}{q_{\max} - q_{\min}}. \quad (\text{A1})$$

Using this, we can solve for the equilibrium plant densities,

$$\frac{d}{dt}p(q) = 0 = r(q)\hat{p}(q) \left[1 - \frac{\hat{p}(q)}{K(q)} - \frac{c_f \hat{h} C(\sigma)}{r(q)(q_{\max} - q_{\min})} \right], \quad (\text{A2})$$

which gives

$$\hat{p}(q) = 0 \quad \text{or} \quad (\text{A3a})$$

$$\hat{p}(q) = K(q) \left[1 - \frac{c_f \hat{h} C(\sigma)}{(q_{\max} - q_{\min})r(q)} \right]. \quad (\text{A3b})$$

The second solution shows that (provided a positive equilibrium is attained) $\hat{p}(q)$ is negatively related to the equilibrium number of herbivores. Note also that $\hat{p}(q)$ is proportional to $K(q)$, owing to nonselective foraging. In turn, the equilibrium number of herbivores

can be expressed by using the equation for $\hat{p}(q)$ in the equilibrium intake rate \hat{I} ,

$$\begin{aligned} \hat{I} &= \frac{c_f C(\sigma)}{q_{\max} - q_{\min}} \int_{q_{\min}}^{q_{\max}} \hat{p}(q) e(q) q dq \\ &= \frac{c_f C(\sigma)}{q_{\max} - q_{\min}} \int_{q_{\min}}^{q_{\max}} e(q) q K(q) \left[1 - \frac{c_f \hat{h} C(\sigma)}{(q_{\max} - q_{\min}) r(q)} \right] dq. \end{aligned} \quad (\text{A4})$$

By splitting up the integral and solving for \hat{h} we obtain

$$\hat{h} = \frac{\int_{q_{\min}}^{q_{\max}} e(q) q K(q) dq - \frac{(q_{\max} - q_{\min}) \hat{I}}{c_f C(\sigma)}}{\int_{q_{\min}}^{q_{\max}} e(q) q K(q) \frac{c_f C(\sigma)}{(q_{\max} - q_{\min}) r(q)} dq}. \quad (\text{A5})$$

These equations cannot be solved explicitly. Therefore, also the invasion fitness of herbivores cannot be determined analytically. Nevertheless, conditions for a mutant to invade a resident population at equilibrium can be established, using the criterion that for invasion to succeed the intake rate of a mutant, I' , must be larger than the equilibrium intake rate \hat{I} (which is the same for mutant and resident and is here for convenience expressed using the mutant's strategy),

$$\begin{aligned} I' &= \frac{c_f C(\sigma')}{q_{\max} - q_{\min}} \int_{q_{\min}}^{q_{\max}} \hat{p}'(q) e'(q) q dq > \hat{I} \\ &= \frac{c_f C(\sigma')}{q_{\max} - q_{\min}} \int_{q_{\min}}^{q_{\max}} \hat{p}'(q) e'(q) q dq. \end{aligned} \quad (\text{A6})$$

Here, $e'(q)$ is the efficiency function of the mutant and $\hat{p}'(q)$ is the equilibrium plant density function for a population of such mutants. This results in the inequality

$$\int_{q_{\min}}^{q_{\max}} \hat{p}(q) e'(q) q dq > \int_{q_{\min}}^{q_{\max}} \hat{p}'(q) e'(q) q dq. \quad (\text{A7})$$

This invasion condition is satisfied when the equilibrium plant densities over all plant qualities are smaller in a population of mutant-type herbivores than in a population of resident-type herbivores (i.e., if $\hat{p}'[q] < \hat{p}[q]$ for all q between q_{\min} and q_{\max}). This is the case when the mutant strategy leads to a higher equilibrium herbivore abundance, as it is shown above that equilibrium plant densities are negatively related to equilibrium herbivore abundance. Therefore, a mutant can invade a resident population if and only if its strategy leads to a higher equilibrium herbivore abundance (or, equivalently, to lower equilibrium plant densities).

APPENDIX 3: OPTIMAL FORAGING ($\alpha \rightarrow \infty$)

At ecological equilibrium, a monomorphic population of herbivores uses the range of plant qualities that form the plateau top of the table-mountain-shaped gain curve, between q_{\min} and q_{\max} (this description and the analysis below readily carry over to situations where the gain distribution dictates a disjunct utilization distribution for the optimal foragers). Therefore, for $q < q_{\min}$ and $q > q_{\max}$, the utilization density vanishes, $u(q) = 0$, and hence the equilibrium plant densities are at their carrying capacities, $\hat{p}(q) = K(q)$. By contrast, for $q_{\min} \leq q \leq q_{\max}$ the utilization spectrum is constant and given by

$$u(q) = \frac{1}{q_{\max} - q_{\min}}. \quad (\text{A8})$$

(We assume no cost of specialization, $c_s = 0$, which means that $C[\sigma] = 1$.) As follows from the assumption of optimal foraging, the gain $g(q)$ is also constant over the utilized range of plant qualities, denoted by g_{\max} . Thus, we can solve for the equilibrium intake rate \hat{I} ,

$$\hat{I} = \int_{q_{\min}}^{q_{\max}} g(q) u(q) dq = \frac{g_{\max}}{q_{\max} - q_{\min}} (q_{\max} - q_{\min}) = g_{\max}. \quad (\text{A9})$$

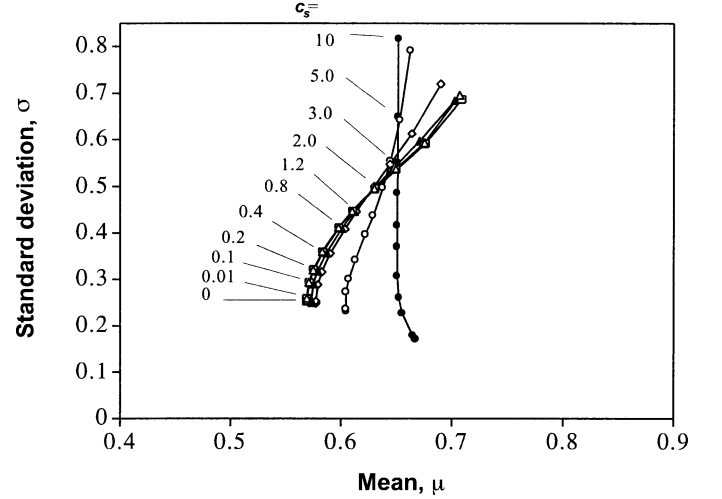


FIG. A1. Evolutionarily singular herbivore strategies (μ , σ) for different foraging accuracies, α , and costs of specialization, c_s . Filled circles: $\alpha = 0.01$; open circles: $\alpha = 0.1$; open diamonds: $\alpha = 0.5$; filled triangles: $\alpha = 1.0$; open squares: $\alpha = 5.0$; open triangles: $\alpha = 10$. Values of c_s as indicated in the figure. Other parameters as in Figure 4.

This equation shows that, at equilibrium, the maximum gain g_{\max} equals \hat{I} .

As in Appendix 2, the equilibrium density of herbivores and plants cannot be solved explicitly. Therefore, to investigate the possibility for mutants to invade, we again have to resort to studying the intake rate. In between q_{\min} and q_{\max} , the gain of a mutant $g'(q)$ for a specific plant quality q is larger than that of the resident when

$$g'(q) = q c_f \hat{p}(q) e'(q) > \hat{I} = q c_f \hat{p}(q) e(q), \quad (\text{A10})$$

which holds for any plant quality for which $e'(q) > e(q)$. Due to the optimal foraging assumption, the mutant can restrict feeding to the plant quality that yields highest gain. This will result in an intake rate higher than \hat{I} when the above inequality holds, allowing such a mutant to invade. For arbitrarily small mutations in either μ or σ , and given that $q_{\max} - q_{\min}$ is not arbitrarily small, this inequality holds: efficiency is higher for plant qualities in the neighborhood of $q = \mu$. When the inequality does not hold, also the plant quality ranges that the resident population does not use ($q < q_{\min}$ and $q > q_{\max}$) should be investigated to check whether at any plant quality the gain exceeds the equilibrium intake rate,

$$K(q) e'(q) q > \hat{I}. \quad (\text{A11})$$

If the whole quality gradient is in use by resident herbivore types, only the first of the above inequalities applies. To be certain that a mutant (μ , σ') can invade, we have to consider its gain at plant quality $q = \mu$. As shown above, this gain exceeds \hat{I} if $e'(\mu) > e(\mu)$, which always applies when $\sigma' < \sigma$ (i.e., for a more specialized mutant).

APPENDIX 4: SUBOPTIMAL FORAGING ($0 < \alpha < \infty$)

Deterministic Approximation

Tracking the singular point of a monomorphic population through trait space for different values of the cost of specialization c_s shows that a higher cost of specialization indeed selects for more generalist phenotypes (Fig. A1). For increasing values of α , the singular strategy is less specialized for low c_s and more specialized for extremely high c_s ($c_s > 3$; see Fig. A1). Whether the singular strategy is an evolutionary branching point also depends on the cost of specialization (Fig. A2). Below a critical cost, evolutionary branching results in specialized herbivore phenotypes. Above the critical cost, the evolutionary dynamics result in a single generalist phenotype.

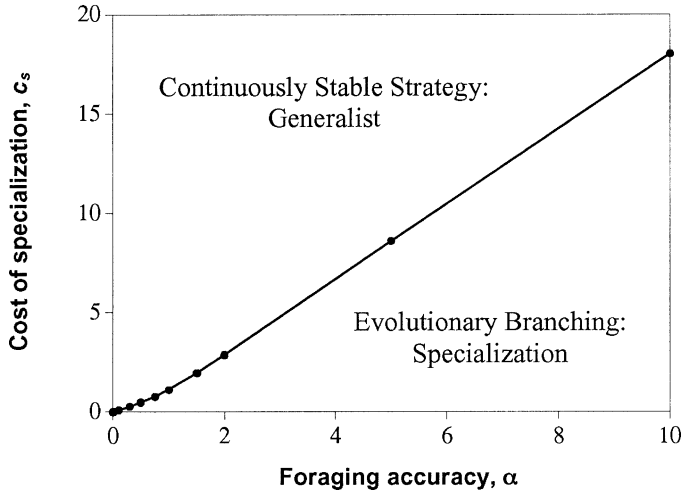


FIG. A2. Critical values of the cost of specialization, c_s , for different foraging accuracies, α . Above the curve, the evolutionarily singular strategy is a continuously stable: at evolutionary equilibrium the population consists of one herbivore phenotype with a generalist strategy. Below the curve, the singular strategy is an evolutionary branching point: here, the population can split up in two or more herbivore phenotypes with increasing degrees of specialization. Other parameters as in Figure 4.

This critical cost is higher if α is higher, i.e., if the herbivores are better foragers.

Individual-Based Model

At the polymorphic evolutionary equilibrium, the number of phenotypes in the herbivore community depends on the degree of suboptimal foraging, α : higher values of α allow for more phenotypes to coexist in the population (Fig. A3a). This is because more selective foragers can better focus their foraging effort, even when they are specialized. At the same time, the phenotypes are less specialized when they are more selective foragers (Fig. A3b). Increasing the cost of specialization decreases the number of phenotypes that can coexist along the plant gradient (Fig. A3a). The number of phenotypes that squeeze into the resource gradient goes down (limiting similarity), because the herbivores evolve a lower degree of specialization when the cost for specialization is higher (Fig. A3b).

The degree of ecological character displacement can be expressed by the d/w ratio (May and McArthur 1972). Here, d is the distance between two adjacent phenotypes, measured by the means μ_i of their efficiency distributions, $d = |\mu_1 - \mu_2|$. Through the d/w ratio, the distance d is then considered relative to the width w of the efficiency distribution of the focal phenotype, which is here taken as the standard deviation σ of the efficiency distribution. In this way, each comparison of a pair of adjacent phenotypes gives two values of the d/w ratio (one for each phenotype) and the total number of d/w ratios is $2(\text{number of branches} - 1)$. The d/w ratio describes displacement in the fundamental niches of the phenotypes, not in their realized niches (which are kept roughly separate, due to their foraging behavior). It turns out that this measure of character displacement remains fairly constant along the plant quality gradient. Values for d/w increase from roughly 2 to 6 as α decreases from 1.0 to 0.1, but are not significantly affected by the cost of specialization (Fig. A3c). The latter result is expected, because this cost does not affect foraging ability, so that the separation between phenotypes along the plant gradient (which is caused by this ability) remains unchanged. Thus, the amount of ecological character displacement of herbivore phenotypes depends critically on their degree of suboptimal foraging behavior.

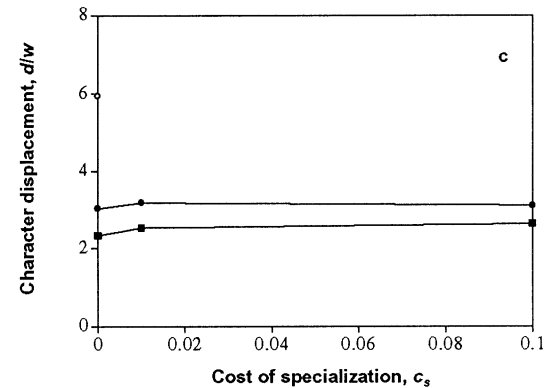
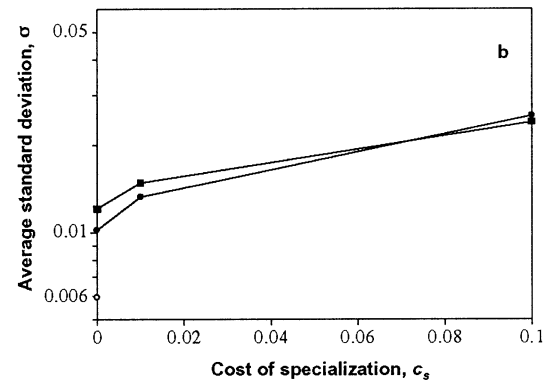
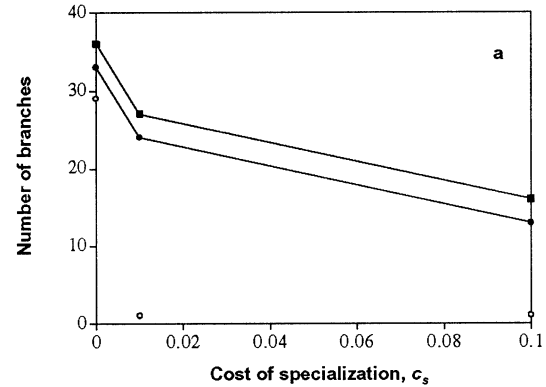


FIG. A3. Characteristics of the polymorphic evolutionary equilibrium for different foraging accuracies, α , and costs of specialization, c_s . (a) Number of phenotypes (open circles: $\alpha = 0.1$; filled circles: $\alpha = 0.5$; filled squares: $\alpha = 1.0$). Note that for $\alpha = 0.1$ evolutionary branching only occurs for $c_s = 0$; therefore, in this case the number of phenotypes is one for $c_s = 0.01$ and $c_s = 0.1$. (b) Average level of specialization σ among the phenotypes. (c) Average character displacement d/w among the phenotypes. Other parameters as in Figure 6.