

Niche co-evolution in consumer–resource communities

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ABSTRACT

Problem: Niche co-evolution deals simultaneously with the number and the character of species within a community. How can a community of predators and prey adaptively radiate to fill available niches? How many niches are there? And, can adaptive speciation at evolutionary branching points successfully fill the niches of the ESS?

Model features: We use a predator–prey model with one fitness-generating function, a *G*-function, for the prey and a separate one for the predators. Species diversity can emerge from within and between the two *G*-functions. Two niche-breadth parameters (prey niche breadth and predator niche breadth) determine the number of prey and predator species at the ESS.

Mathematical method: To identify the ESS community for a given pair of niche parameters, we use a numerical approach. All possible strategies can invade at all times. We also apply adaptive dynamics, adaptive speciation, and the invasion of completely novel species to see how a starting community of a single prey and a single predator species can radiate to become the ESS community.

Conclusion: In the absence of speciation or species invasions, adaptive dynamics cause the existing species to evolve to convergent stable niche archetypes. These archetypes may be local ESS strategies or evolutionary branching points (i.e. convergent stable fitness minima). Initially, adaptive speciation at branching points suffices to increase diversity from one set of niche archetypes to the next. On approaching the ESS community, speciation at one trophic level makes possible further diversification at the other trophic level. The final species to complete an ESS community may require invasions from species with quite different strategy values to those present in the community. In the state space of prey and predator niche breadth, we can plot regions of iso-diversity for the ESS communities of prey and predators.

Keywords: adaptive radiation, co-evolution, evolutionarily stable strategy, evolutionary dynamics, fitness-generating function, niche archetypes, niche co-evolution, species diversity.

INTRODUCTION

Evolutionary game theory provides a framework for modelling niche co-evolution within communities. We expect organisms under natural selection to evolve optimal strategies that maximize fitness, given the circumstances. Such strategies may be complex genetic and

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phenotypic traits. Instead of penetrating the background of these traits, they can be modelled as strategies evolving through natural selection along landscapes, mapping strategy space onto fitness. Under frequency- and density-dependent selection, the adaptive landscape changes continuously with changes in strategy frequencies and densities, giving rise to an ecological and evolutionary 'feed-back environment' (Metz *et al.*, 1992; Heino *et al.*, 1998). Still, evolutionary games, once defined, tend to possess evolutionarily stable strategy (ESS) solutions (Maynard Smith, 1982; Geritz *et al.*, 1998), and it is of interest to know when such solutions can be the anticipated endpoint of evolution.

Theories of niche patterning are not comprehensive with respect to ecological and evolutionary processes. Theories of limiting similarity (MacArthur and Levins, 1967; May, 1973; but see Kisdi and Geritz, 2003) consider the ecological feasibility of co-existence to be influenced by the degree of niche partitioning, without recourse to whether natural selection actually favours convergent or divergent evolution among competitors. Assembly rules (Diamond, 1975; Brown *et al.*, 2002; but see Morris, 2003) consider how communities might build up in their niche characteristics with successive additions of species without explicit ecological or evolutionary dynamics. Many models of co-evolution, game theoretic or otherwise, fix the number of species and then see how niche characteristics co-evolve. All of these theories progress ideas towards addressing fundamental questions: How many niches does a community have? Are communities under- or over-saturated with species? How do invasion-structured communities differ from co-evolved communities? And, what role does adaptive speciation (Maynard Smith, 1966; Rosenzweig, 1978; Dieckmann and Doebeli, 1999; Schluter, 2001) play in the diversification of communities?

Evolutionary game theory makes it possible to expand the role of natural selection in the modelling of niches and niche co-evolution. Starting with a simple model of population interactions, it is possible to embed an evolutionary strategy into the model's parameters. In this game, both the diversity of strategies and their values can evolve and change with time. Through evolutionary branching it is possible to see both co-evolution and species diversification within, for instance, the Lotka-Volterra model of competition (Vincent *et al.*, 1993; Geritz *et al.*, 1998; Cohen *et al.*, 1999). Once specified, the evolutionary game surrounding a model of population interactions sets the diversity and characteristics of strategies at the ESS. The ESS must be diverse enough to be resistant to invasion by any rare alternative strategy, and yet not so diverse as to preclude the co-existence of all of the different strategies.

Here we are interested in how processes of diversification and co-evolution can lead to a system's ESS community, even when initial conditions involve numbers of species far below those required for the ESS. There are several processes that can drive the community towards its ESS: concurrent co-evolution of existing strategies, adaptive speciation (Rosenzweig, 1978; Brown and Pavlovic, 1992; Dieckmann and Doebeli, 1999), and invasion of species from outside the community (Brown and Vincent, 1987). Here we ask: Can, and will, these processes actually make the community attain its ESS? In achieving the ESS, is there a regular sequence in the addition of species (like assembly rules)? How do population and evolutionary dynamics change as the ESS is approached?

We also investigate the diversity of the ESS community as influenced by the underlying ecological parameters, especially the niche widths of the prey and predators. Does a narrow niche width – that is, higher specialization – inevitably lead to increased biodiversity? How is predator diversity related to prey niche width and vice versa?

We investigate these questions in a damped Lotka-Volterra predator-prey model. The model generates a variety of ESSs that vary in the number of prey and predator species.

Brown and Vincent (1992) sought the ESSs of a similar model but did not investigate the nature of niche evolution that would be necessary to achieve the ESSs. Furthermore, here we will vary the range of niche-breadth characteristics of the prey and predators in a manner where the prey can drive prey diversification, predators can drive prey diversification, and prey can drive predator diversification. In what follows, we (1) develop the model, (2) find and characterize the ESSs of the model, and (3) use evolutionary dynamics to determine whether adaptive speciation (evolutionary branching) and co-evolution can radiate the community to an ESS.

THE MODEL

We use a discrete time Lotka-Volterra predator–prey model with logistic growth of the prey. The model has few parameters, yet it includes the most important ecological interactions. We will transform this model into fitness-generating functions, or G -functions, by starting with the ecological dynamics and incorporating the individual's evolutionary strategy, the strategies of others, and the population sizes of the different extant strategies (Vincent and Brown, 2005).

We start with prey and predator population dynamics driven by the following discrete time equations:

$$N_{t+1} = N_t f_1(N_t, P_t) = N_t(1 + r(1 - N_t/K) - bP_t) \quad (1)$$

$$P_{t+1} = P_t f_2(N_t, P_t) = P_t(1 - \mu + cbN_t) \quad (2)$$

where N and P are the prey and predator population sizes respectively, r is the intrinsic population growth rate of the prey, K is the prey's carrying capacity, b is the per capita probability of capture by a predator per time unit, μ is predator mortality, and c is a conversion factor from prey to predators. The discrete time formulation induces a time delay in the ecological feedback, which is usually not present in similar continuous time models. This time delay sometimes causes over-compensatory dynamics and potentially negative population sizes, but this is prevented by a truncation of equations (1) and (2) at zero (as well as equations 8 and 9 below). More importantly, time delays are ubiquitous in ecological systems and we therefore do not think our model is less appropriate or realistic than a corresponding continuous time model.

To model the interactions among species with different strategies, we generalize the per capita growth rates above (f_1 and f_2) to fitness-generating functions, G -functions. We thus let the fitness of a focal strategy be influenced by the strategies of resident prey and predators, as well as their respective population densities. We denote the vector of strategies found among the prey and predators as $\mathbf{u} = (u_1, \dots, u_m)$ and $\mathbf{v} = (v_1, \dots, v_n)$ respectively, and their corresponding population densities $\mathbf{N} = (N_1, \dots, N_m)$ and $\mathbf{P} = (P_1, \dots, P_n)$ respectively. Finally, we want the G -function to return the fitness expectation of any individual playing a given strategy (u or v), which we will refer to as the focal strategy (Vincent and Brown, 1988). We let the strategy of a focal prey individual, u , influence its carrying capacity, $K(u)$, its competitive interaction with other prey individuals u_i , $a(u, u_i)$, and its capture susceptibility by a given predator strategy v_j , $b(u, v_j)$. The strategy of the focal predator, v , influences its capture success on a given prey strategy u_i , $b(u_i, v)$. We assume that the different strategies of the prey and predator strategy vectors, $\mathbf{u}$ and $\mathbf{v}$, represent different species, not a polymorphism within one species.

These assumptions result in one fitness-generating function for the prey, G_1 , and one fitness-generating function for the predators, G_2 .

Prey:

$$G_1(u, \mathbf{u}, \mathbf{v}, \mathbf{N}, \mathbf{P}) = 1 + r_1 \left(1 - \frac{\sum_{i=1}^m a(u, u_i) N_i}{K(u)} \right) - \sum_{j=1}^n b(u, v_j) P_j \quad (3)$$

Predator:

$$G_2(v, \mathbf{u}, \mathbf{v}, \mathbf{N}, \mathbf{P}) = 1 - \mu + c \sum_{i=1}^m b(u_i, v) N_i \quad (4)$$

We use Gaussian functions to define how the respective strategies influence carrying capacity, competition, and predation rates:

$$K(u) = K_{\max} e^{-\frac{u^2}{2\sigma_K^2}} \quad (5)$$

with maximum value $K_{\max}$ at $u = 0$ and resource breadth σ_K ,

$$a(u_1, u_2) = e^{-\frac{(u_1 - u_2)^2}{2\sigma_a^2}} \quad (6)$$

with maximum value 1 at $u_1 = u_2$ and prey niche width σ_a ,

$$b(u, v) = b_{\max} e^{-\frac{(u - v)^2}{2\sigma_p^2}} \quad (7)$$

with maximum value $b_{\max}$ at $u = v$ and predator niche width σ_p .

A prey maximizes its carrying capacity by possessing $u = 0$. We assume that, among the prey, like competes most intensively with like. Thus, the competition function is symmetric and centred at $u_1 = u_2$. We also assume the predators have a best matching strategy for capturing prey. The capture probability function is centred at $u = v$, where the predator has the matching strategy to that of the prey individual.

The G -functions can be used to determine the per capita growth rate of any population in the community, expressed as a function of present strategies and population densities. The complete expressions for (1) and (2) now become

$$N_i(t+1) = N_i(t) G_1(u_i, \mathbf{u}, \mathbf{v}, \mathbf{N}(t), \mathbf{P}(t)) \quad i = 1, \dots, m \quad (8)$$

$$P_j(t+1) = P_j(t) G_2(v_j, \mathbf{u}, \mathbf{v}, \mathbf{N}(t), \mathbf{P}(t)) \quad j = 1, \dots, n \quad (9)$$

which comprises a full food web model of m prey and n predators.

ADAPTIVE LANDSCAPES AND FINDING THE ESS

In this section, we discuss sources of species diversity within an ESS, how to find the model's ESSs, and the properties of these ESSs.

The model implements several sources of species diversity at the ESS via the width of the prey's resource base, σ_K , the prey's competition breadth, σ_a , and the predator's niche

breadth, σ_p . The prey experience two sources of disruptive selection. The first comes from the competition coefficient in which a given prey competes most strongly with its conspecifics. Any unilateral deviation in strategy by a focal prey will reduce its competition with conspecifics. The strength of this disruptive selection decreases with the prey niche breadth σ_a . With low values of σ_a , competition intensity decreases rapidly with increasing distance between strategies. The second source of disruptive selection is predators possessing the exact matching strategy for a given prey species. Any deviation in strategy by the prey in response to the predator's best matching strategy will reduce the prey's mortality to the predator. The strength of this disruptive selection decreases with the predator niche breadth σ_p . Reductions in the prey and predator niche breadths promote higher species diversity at the ESS.

The width of the prey's resource base, σ_K , counterbalances the disruptive selection. In the model, a strategy value of zero always maximizes a prey's resource utilization. Deviations from zero reduce a strategy's carrying capacity. The magnitude of this reduction declines with σ_K . A narrow resource base for the prey (low value for σ_K) produces very strong stabilizing pressure on $u = 0$. With a broader resource base, the pressure declines, and there is a higher likelihood that the ESS will support prey strategies further from zero.

The predators' evolution depends on selection pressure exerted by their prey. The predators are under selection to follow the strategies of the prey. This directional selection by the predators chasing a prey's strategy and the prey running away from the predator's strategy can set off a Red Queen race. Two processes oppose this Red Queen process. First, the prey may stop 'running' as the prey's strategy balances selection from the predator, other prey, and its own carrying capacity. Second, if there is more than one prey strategy, the predator may be under disruptive selection from prey strategies on either side of its own. When there are several prey species, decreasing the predator's niche breadth, σ_p , increases the strength of the disruptive selection exerted by several prey species on the predator. The predator's niche breadth influences its tendency to evolve generalist strategies in response to diverse prey species or to specialize on particular prey species.

The relative magnitudes of these three parameters – the breadth of the resource base, σ_K , and the prey and predator niche breadths, σ_a and σ_p – determine the character and diversity of the ESS community. Without loss of generality, we will fix σ_K to 1 and vary the other two parameters. For completeness, it should be noted that the parameters $K_{\max}$, $b_{\max}$, c , and μ also influence the number of species at the ESS community. For instance, $K_{\max}$ too low will make any predator population unsustainable. As our interest is in niche partitioning, we focus on the two niche width parameters described above, assuming the qualitative patterns we find are robust to moderate changes of the other model parameters.

We used simulations to find candidate solutions for the ESS, and then verified the ESS necessary conditions by inspecting the shape of the adaptive landscape at the candidate solution. Our simulations started with 501 prey and 501 predator strategies with equal population sizes distributed at small intervals along the full continuum of evolutionarily feasible strategies for prey and predator, respectively ($-5 \leq u, v \leq 5$). We then used the G -functions to evaluate each resident strategy's per capita growth rate and its new population density (equations 8 and 9). We iterated the population dynamics by substituting the new population densities into the G -functions for further changes in population densities. This iterative process eventually approached an equilibrium with a number of strategies stabilizing on positive population sizes with fitness values of 1. When G is plotted against strategy values at the equilibrium, the resulting adaptive landscape reveals an ESS

solution if the extant strategies (those with non-trivial population sizes) take on global peaks of 1 on the landscape. To avoid the possibility of any strategy within the spectrum getting lost prematurely, a small, trivial population size of 1×10^{-4} was given as the lower limit for any strategy's population size. A population for which the adaptive landscape changes from a valley to a peak could start to increase again. Thus, at any point in time any strategy could 'invade' the community should it be selected for.

An ESS must also be convergent stable to be of evolutionary relevance (Eshel and Motro, 1981). Adaptive dynamics must drive the species' strategies back to their ESS values given small perturbations in the species' strategy values. We evaluated convergence stability numerically by calculating the Jacobian matrix of the adaptive dynamics (see below and the Appendix). If the eigenvalues of the Jacobian all have negative real parts, we verify convergence stability. All ESS configurations accounted for here (Figs. 1–5) are convergent stable. It should, however, be noted that convergence stability to some extent depends on quite arbitrary assumptions, such as the relative speeds of predator and prey evolution (Marrow *et al.*, 1996).

Example adaptive landscapes are shown in Fig. 1. At the ESS, the number of peaks, the relative height of hills to valleys, and the total range of extant strategies at the ESS vary

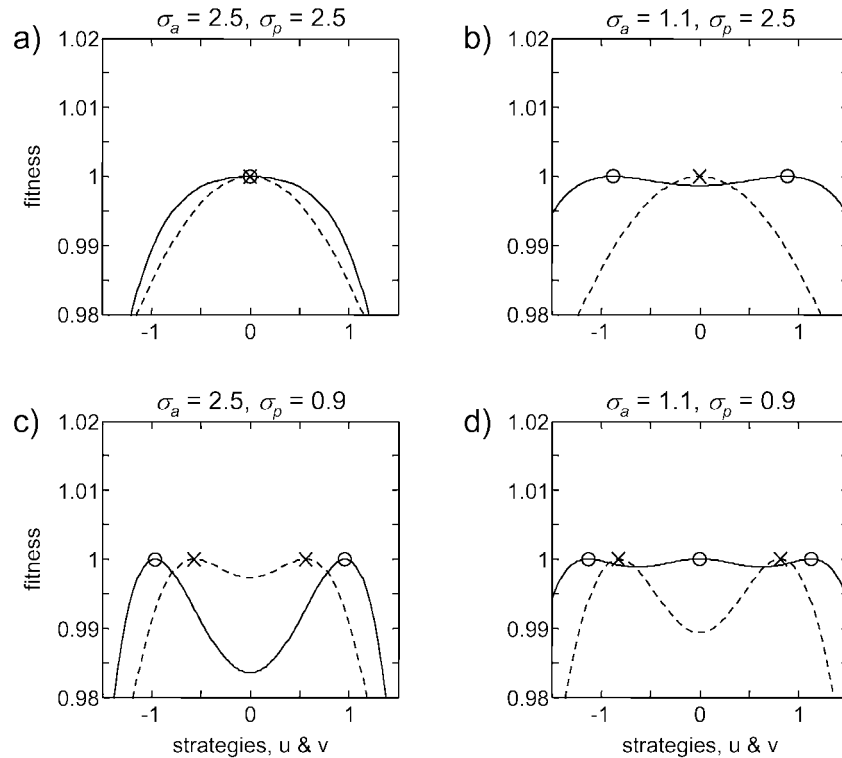


Fig. 1. Adaptive landscapes of the ESS configurations of prey and predators. The prey fitness function (solid line) has local maxima at the prey ESS strategies (circles) and predator fitness (dashed line) has maxima at the predator ESS strategies (crosses). The different panels show the ESS communities at different values of prey and predator niche breadths (σ_a and σ_p , respectively), as indicated above the panels. Other parameter values: $\sigma_K = 1$, $K_{\max} = 100$, $b_{\max} = 0.1$, $r = 0.25$, $\mu = 0.2$, and $c = 0.1$.

with the niche widths of the prey (σ_a) and predators (σ_p). With $\sigma_a = \sigma_p = 2.5$, the stabilizing selection pressure on the prey dominates, and the ESS community possesses just one predator and one prey strategy (Fig. 1a). When the prey's niche breadth σ_a is decreased, competition will decline faster with distance in strategy space, and the intensified disruptive selection produces an ESS of two prey species and a generalist predator species (Fig. 1b). By instead decreasing the predator niche breadth σ_p , the predator can select for two prey species as the prey escape risk from a single generalist predator. The two prey, in turn, create disruptive selection on the predator, which results in an ESS with two prey species and two specialized predator species (Fig. 1c). Finally, when both σ_a and σ_p are decreased, the ESS achieves a higher diversity with three prey species and two predator species (Fig. 1d). Without predators, $P = 0$, the same set of parameter values illustrated here invariably result in a single prey ESS strategy (Christiansen and Loeschke, 1980).

The niche breadth parameters form a two-dimensional parameter space. Each point in this space results in a particular diversity of prey and predator species at the ESS. Hence, we can identify regions of equal species diversity in this state space. Small, continuous shifts in the parameters will not necessarily shift species diversity, as diversity is discrete. Changes of sufficient magnitude will, however, shift the system from one region of diversity into another. Figure 2 plots these regions of equal biodiversity and shows how species numbers at the ESS vary within the parameter space. The narrower the niche breadths, the more strategies are present at the ESS. For this model, the ESS solution never contains more predator species than prey species. We kept the width of the resource landscape fixed ($\sigma_K = 1$). A change of σ_K would be equivalent to a rescaling of the other two parameters, i.e. moving along a straight line through the origin in Fig. 2, such that the ratio σ_p/σ_a is kept constant. An increase in σ_K corresponds to moving towards the origin along such a line. Hence, increasing the resource breadth, σ_K , increases the species diversity of both prey and predators. The number of prey species increases because a wider resource landscape allows for a greater diversity of prey strategies. Predator diversity increases as a consequence of the increased prey diversity.

The number of prey strategies (Fig. 2a) depends heavily on both prey niche breadth, σ_a , and predator niche breadth, σ_p . As described above, a narrow predator niche will impose disruptive selection on the prey, promoting prey diversification. The number of predators, on the other hand, depends primarily on σ_p (Fig. 2b). The same reasoning applies here as to the diversification of the prey through a decreased prey niche width. A generalist predator with a wide niche can monopolize several tightly packed prey species, excluding alternative predator strategies. To such a predator, the prey appear as a continuous distribution of resources rather than distinct peaks on a resource landscape. As a consequence, predator diversity becomes somewhat independent of the prey niche breadth and the corresponding prey diversity. As the predator niche width is decreased, competition between different predator strategies will decrease, allowing for a more diverse predator community. The prey niche width, σ_a , has a noteworthy effect on predator diversity only when the number of prey species sets an upper limit to the number of possible predators, as is the case when the predator niche, σ_p , is narrow relative to the prey niche, σ_a (see lower parts of Fig. 2). Another mechanism by which predator diversity can remain low despite a large number of prey is when several prey populations are too small to support a predator population. More precisely, the predator invasion fitness (equation 4) has to be larger than 1 for any potential (specialist) predator to invade, and this is not the case if prey equilibrium density is too low. If σ_a is small, a great number of new prey strategies will occur within the tails of the

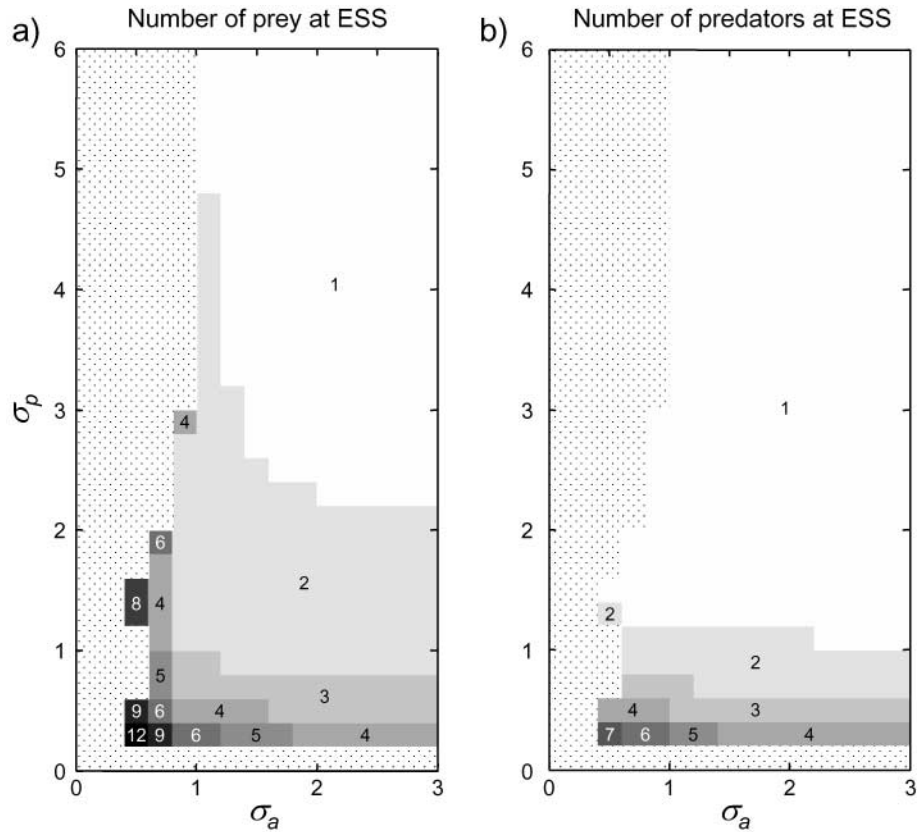


Fig. 2. A survey of the diversity at the two trophic levels as a function of consumer niche breadth (σ_a) and predator niche breadth (σ_p). The number of prey species (left) and predator species (right) at the ESS configuration are indicated with grey scale and numbers in each region. Stippled areas indicate that no ESS was found, either because the strategy dynamics (see text) never settled on a fixed set of peaks (mostly on the left-hand side) or because the resolution of strategy values in the simulations was insufficient (along the lower edge in the graphs). Other parameter values as in Fig. 1.

resource distribution. Here, carrying capacity is low, precluding the existence of predators specializing on these marginal prey. Instead, the predators specialize on the more abundant prey species occupying the central area of the resource distribution.

Finally, it should be noted that the number of species at the ESS depends on other model parameters as well, but numerical investigations suggest that the qualitative patterns presented in Fig. 2 are robust to at least moderate changes in those parameters (still allowing for predator existence, for example).

EVOLUTIONARY DYNAMICS AND NICHE CO-EVOLUTION

The previous section identified the ESSs. Now, can we model an adaptive radiation of prey and predator species? In this section, we examine whether adaptive dynamics and adaptive speciation [evolutionary branching (Geritz *et al.*, 1998)] can produce the ESS community from a starting community of one prey and one predator species.

The adaptive dynamics are defined as a change in strategy value in response to the current gradients of the adaptive landscape. These gradients are defined by the partial derivative of the G -function with respect to the strategy of the focal individual ($\partial G_1/\partial u|_{u=u_i}$ for each $u_i \in \mathbf{u}$; and $\partial G_2/\partial v|_{v=v_j}$ for each $v_j \in \mathbf{v}$). Under this dynamic, the strategy value changes in the direction of the slope of the adaptive landscape, with a rate of change proportional to the magnitude of the slope (Iwasa *et al.*, 1991; Abrams *et al.*, 1993a; Vincent *et al.*, 1993) and population size (Dieckmann and Law, 1996). These changes occur on an evolutionary time scale. To set the population sizes for the strategy dynamics, we assume that the ecological time scale of population dynamics is faster than the evolutionary time scale of strategy dynamics (Geritz *et al.*, 1998; Cohen *et al.*, 1999). We let evolutionary change occur as

$$\Delta u_i = \delta_1 N_i \left. \frac{\partial G_1}{\partial u} \right|_{u=u_i} \quad (10)$$

$$\Delta v_j = \delta_2 N_j \left. \frac{\partial G_2}{\partial v} \right|_{v=v_j} \quad (11)$$

where $\delta_1 = 5 \times 10^{-4}$ and $\delta_2 = 5 \times 10^{-3}$. According to the canonical equation of adaptive dynamics (Dieckmann and Law, 1996), δ_k ($k=1,2$) equals $\frac{1}{2}\mu_k\sigma_k^2$, where μ_k is the mutation probability per individual and σ_k^2 is the corresponding variance of mutational effects. Between each evolutionary time-step (equations 10 and 11), we allow for one time-step of population dynamics according to equations (8) and (9). By choosing the δ_i small, we ensure that the populations remain close to the equilibrium population sizes for the current mix of species and strategies or, more generally, close to the current population dynamic attractor. The predators are given a higher potential for evolutionary rate of change than the prey ($\delta_2 = 10\delta_1$). This can be interpreted as the predator strategy is a trait with higher genetic variance (per capita), higher mutation rate or higher variance of mutational effects. This difference in ‘evolvability’ is necessary here to ensure convergence stability of the first evolutionary branching points – in an unsaturated community the prey, having a larger population size and plenty of available niche space, can otherwise outrun the predators in an evolutionary arms race and the predators will go extinct or, alternatively, get caught in cyclic Red Queen evolutionary dynamics (Marrow *et al.*, 1996).

With a fixed number of species, adaptive dynamics will drive the species’ strategies to points of convergence stability, which we call *niche archetypes*. A given strategy may evolve to either a local maximum (evolutionarily stable maximum) or a local minimum. A convergent stable minimum (i.e. an evolutionary branching point) allows for polymorphism and possible speciation (Christiansen and Loeschke, 1980; Brown and Pavlovic, 1992; Abrams *et al.*, 1993b; Dieckmann and Doebeli, 1999; Ripa, 2009). We let adaptive speciation occur whenever the evolutionary dynamics places a strategy at a branching point. With speciation, we add a new species with a strategy value very close to the extant species ($\Delta u = 0.02$). With two species occupying the same valley, their strategies will diverge up opposite slopes of the adaptive landscape (Geritz *et al.*, 1998; Cohen *et al.*, 1999). On many occasions, several species reached evolutionary branching points simultaneously, and we had to choose which species should speciate. However, we never noticed any effect of our arbitrary choice on the ensuing adaptive radiation. The community converged to the same set of strategies, the same niche archetypes, no matter which species we chose as the ‘parent’ species.

In the following simulations, we let evolutionary dynamics evolve strategy values to convergent stable points. We let adaptive speciation occur for species at convergent stable minima. Together, these two processes generate an adaptive radiation, niche filling, and niche co-evolution. In each simulation, the system was initiated with one predator and one prey strategy. The prey strategy was placed at the value that maximizes carrying capacity: $u = 0$. The starting predator's strategy matched that of the prey: $v = 0$. As will be seen in the simulations, the ecological dynamics, for any given set of extant predator and prey strategies, could lead to a stable equilibrium or limit cycles.

The process of evolutionary dynamics and sympatric speciation was repeated until either the community converged on a set of convergent stable maxima, or until the numbers and positions of predator and prey species attained the ESS. If species' strategies reside at non-ESS local maxima, then we had to introduce a new species with a strategy far from the extant strategies to continue evolution towards the ESS. Such an invasion cannot be the product of sympatric speciation, but may be thought of as an invasion of a species that has evolved elsewhere via allopatric speciation.

Figures 3 and 4 show the changes in the numbers of species, and changes in their strategy values and population sizes, as evolution proceeds from one prey and one predator species towards the ESS communities. New species were added to the communities as specified by our speciation 'rules' above. To facilitate the interpretation of these graphs, the introduction of each new species and its strategy values is labelled with a sequential number. Every time a new species is introduced, its path shows whether it succeeds in the community. If successful, its strategy value will co-evolve away from its source value and its population size will increase. A strategy that cannot invade will re-converge to its source and its population size will approach zero.

The progression of adding new species and following their co-evolution varies with parameter values, but there are some common features. In the beginning, far from the ESS, the communities are highly unstable, both ecologically and evolutionarily. The introduction of new strategies and the subsequent evolution alters the adaptive landscape dramatically. When approaching the ESS, the communities stabilize and change more slowly, and the adaptive landscape becomes correspondingly more rigid. With increasing rigidity, and flatness, of the landscape, sympatric speciation or invasion by a new strategy takes longer. Once the adaptive radiation and niche filling is complete, the species of the ESS communities exhibit stable strategy values and population sizes.

Figure 3a shows the adaptive landscape at an ESS community of three prey and three predator species. The corresponding population sizes (right-hand y-axis) are shown as bars. Figures 3b and 3c show the evolutionary route to that community. In this example, the prey niche width is wide ($\sigma_a = 2.6$) but the predator niche is narrow ($\sigma_p = 0.5$). Hence, predation will be the major force driving the adaptive radiation. From a prey's perspective, avoiding predation is easy, whereas avoiding competition is hard, since competition coefficients decrease very slowly along the resource axis. From a predator's perspective, it is easy to avoid competition for prey since all predators are specialized on a narrow range of prey.

In the beginning, the single prey species faces strong disruptive selection due to the specialized strategy of the single predator species. The prey reside at an evolutionarily stable minimum of their adaptive landscape. As a second prey is introduced (1), the disruptive selection co-evolves the two prey strategies apart. The predator first evolves to specialize on one of them, but later evolves to a strategy in between the two prey species. We have a generalist predator. Under this convergent stable configuration, the predator experiences

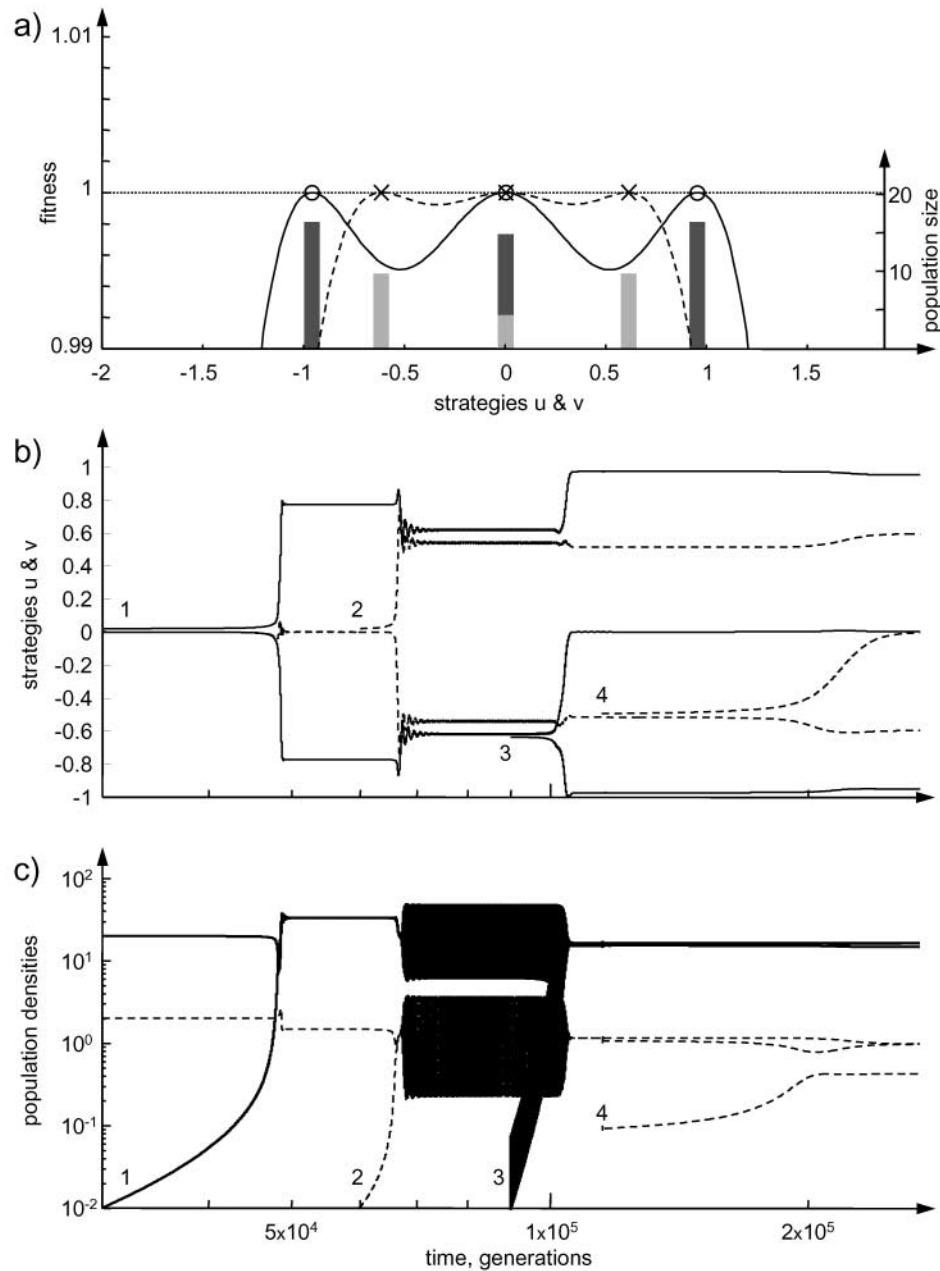


Fig. 3. ESS landscape (a), evolutionary dynamics (b), and population dynamics (c) as the result of a simulation with the evolutionary dynamic model, where $\sigma_a = 2.6$ and $\sigma_p = 0.5$. Solid black lines represent prey and dashed grey lines predator fitness landscapes, strategy values, and population densities, respectively. The filled bars in (a) show the equilibrium population sizes (right y-axis) of prey (dark grey) and predators ($\times 10$, light grey). The numbers 1–4 in (b) and (c) represent the introduction of new strategies and are referred to in the text. The evolvability parameters are set to $\delta_1 = 5 \times 10^{-4}$ and $\delta_2 = 5 \times 10^{-3}$ (cf. equations 10 and 11). Other parameter values as in Fig. 1.

disruptive selection from the strategies of the two surrounding prey species. The prey reside on peaks of their adaptive landscape and the predator species resides at an evolutionarily stable minimum.

The introduction of a second predator strategy (2) leads to the evolutionary divergence and specialization of two predator species, each specializing on a different prey species. With this new predator species and subsequent co-evolution of all four species, the evolutionary dynamics stabilize, but the population dynamics do not. The populations start to fluctuate with high amplitude cycles. These fluctuations represent non-equilibrium population dynamics that are not in response to non-equilibrium evolutionary dynamics (save for negligible fluctuations). Hence, even with the unstable population dynamics, the evolutionary dynamics stabilize on a convergent stable point [for discussion of ESSs under non-equilibrium population dynamics, see Vincent and Brown (1986)]. The prey reside at very shallow minima of their adaptive landscape, while the predators reside on peaks. With the addition and subsequent evolution of a third prey species (3), the population dynamics stabilize. The prey co-evolve to peaks and the predators co-evolve to convergent stable valleys of their adaptive landscapes. The introduction of a third predator species (4) allows the community to fill the niches of the ESS.

This adaptive radiation of three prey species and three predator species from a single prey and predator species can be achieved solely through co-evolution to niche archetypes and adaptive speciation. The succession of four non-ESS niche archetypes exhibit either the prey or the predator residing at evolutionarily stable minima of the adaptive landscape. The introduction of a new species near a species at one of these minima allows the system to co-evolve towards a new, more diverse, set of niche archetypes.

Another example of an evolving community is seen in Fig. 4. Here, both niche widths are narrow ($\sigma_a = 0.6$ and $\sigma_p = 0.5$). The adaptive radiation is driven by both predation and competition. The ESS consists of seven prey and four predator strategies (Fig. 4a). With the successive introduction of new prey (1, 3, 5, 7) and predators (2, 4, 6), a community is reached where no new species can be added close to the extant species – they all reside on local fitness maxima – but the community is not at its ESS. To be able to reach the ESS, the most extreme strategies have to be ‘forced’ into the community, close to their ESS values but far away from any existing strategy (9, 10). A new prey species too close to the extant ones quickly goes extinct (8). Filling the last two marginal niches cannot be achieved unless the community already consists of all possible strategies in between. Hence, not only is the ESS community pre-defined, but so is the order in which the community is assembled.

Under pre-ESS conditions, a community can be wide open to invasion by non-resident strategies that can use either an ‘empty’ portion of the prey’s resource axis (in the case of prey invasions) or an under-utilized and abundant prey species (in the case of predator invasions). The invasion of a species different from all other species of the community has a large effect on the whole community and its immediate evolution. Figure 5a shows a pre-ESS constellation of niche archetypes, corresponding to the community before the second predator speciation (4) in Fig. 4. The prey community is resistant to invasions, save for marginal strategies (very little would change in Fig. 5 if we included the two marginal prey strategies as well). Introducing a predator close to an existing predator strategy has very little immediate effect on the adaptive landscape. If, however, an invading predator has a strategy far from the extant species, its presence will dramatically change the ecological equilibrium and adaptive landscape of both prey and predators. Figure 5b shows the

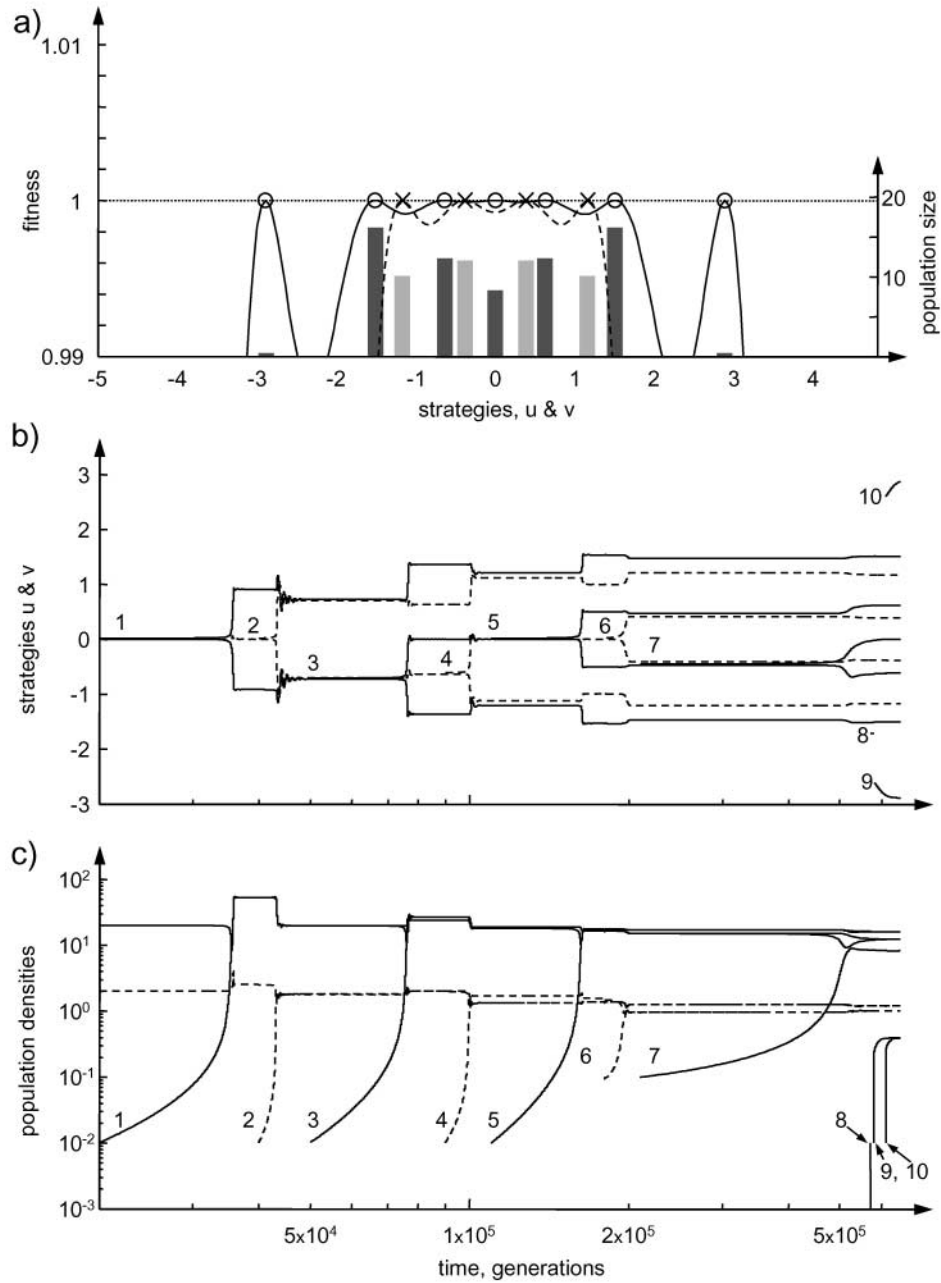


Fig. 4. ESS landscape (a), evolutionary dynamics (b), and population dynamics (c) as the result of a simulation with the evolutionary dynamic model, where $\sigma_a = 0.6$ and $\sigma_p = 0.5$. Solid black lines represent prey and dashed grey lines predator fitness landscapes, strategy values, and population densities, respectively. The filled bars in (a) show the equilibrium population sizes (right y-axis) of prey (dark grey) and predators ($\times 10$, light grey). The numbers 1–10 in (b) and (c) represent the introduction of new strategies and are referred to in the text. Other parameter values as in Fig. 3.

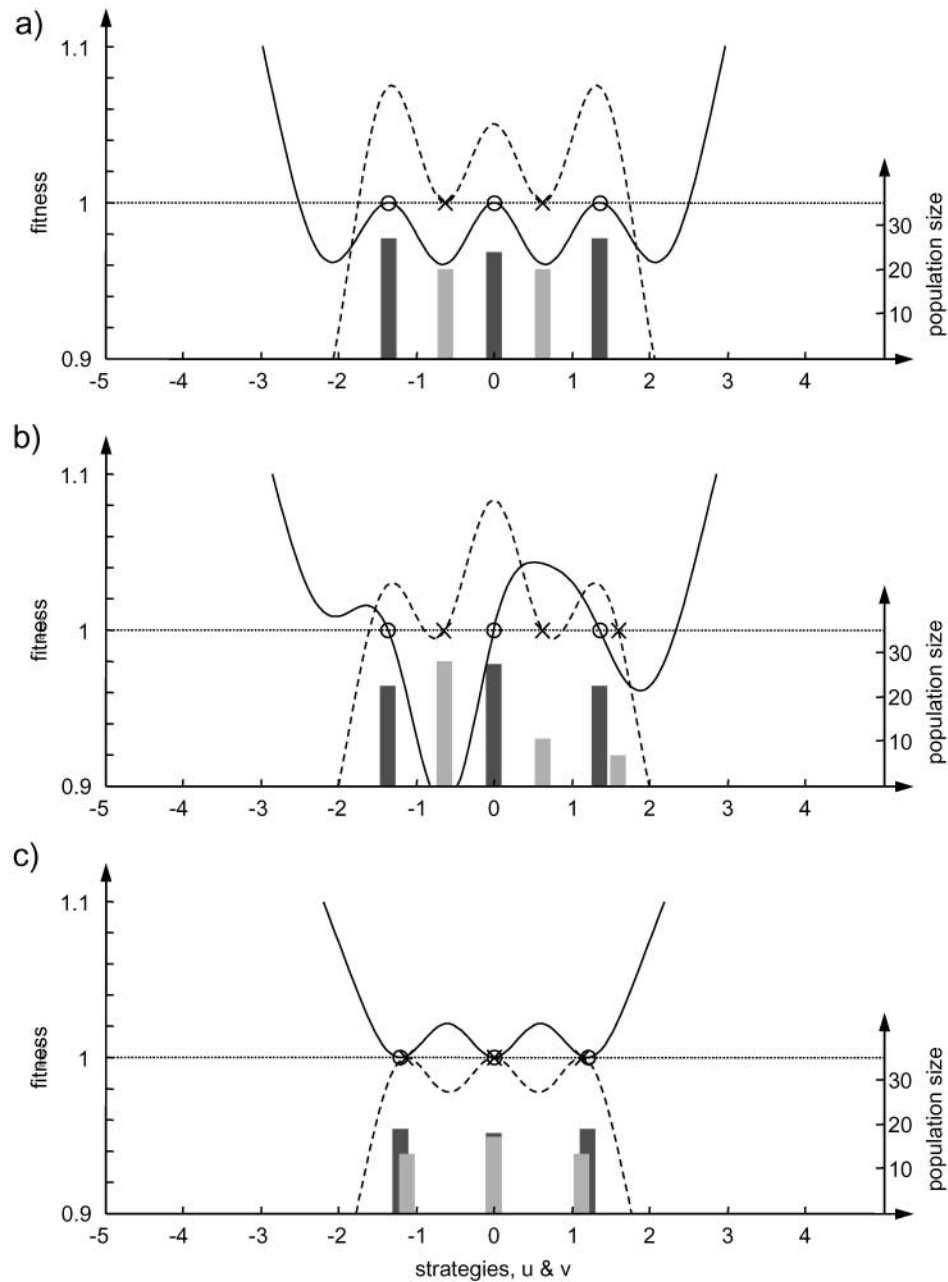


Fig. 5. Pre-ESS constellations of niche archetypes of the same community as in Fig. 4, demonstrating the changes of the adaptive landscape following the introduction of a new strategy. (a) The community before the introduction of the third predator, (4) in Fig. 4; (b) the ecological equilibrium after introducing a new predator at $v = 1.6$, some distance in trait space from the already present predators; and (c) the new evolutionary equilibrium, equivalent to the situation before the introduction of the fourth prey, (5) in Fig. 4. Colour coding, etc., like Fig. 4a, but note the changed scale of the fitness landscape (left y-axis).

ecological equilibrium after such an introduction. The prey community is no longer resistant to invasion and the two predators are no longer at branching points. None of the species is at evolutionary equilibrium – all are subject to directional selection. After convergence to the new niche archetypes (Fig. 5c), all predators reside on fitness peaks. The predator community is now closed to invasions. Instead, the prey community is wide open – anything can invade. The situation in Fig. 5c corresponds to the community just before the introduction of the fourth prey (5) in Fig. 4, which demonstrates how the sequence of niche archetypes is robust to invasions from the outside.

DISCUSSION

We have studied a model of predator–prey co-evolution, exploring a diverse array of ESS communities. The numbers of prey and predator species at the ESS emerged from varying the relationship between three parameters: the width of the prey resource base, prey niche width, and predator niche width. By broadening the prey's resource base or narrowing its niche, the number of prey species at the ESS tends to increase. This increase of prey species and subsequent divergence of their strategies can drive a diversification of predators at the ESS. In contrast, narrowing the predator's niche results in the predators driving the diversification and divergence of prey and predator species at the ESS. The number of prey and predator species is well-defined and given by the model parameters. Consequently, in the trait space of niche width parameters, we can plot the prey and predator species diversity of the ESS. This produces a plot of isodiversity regions, showing all of the combinations of niche width parameters producing the same diversity of species at the ESS. In this context it should be noted that multiple ESS solutions are possible, such that an evolving community has alternative endpoints. We found no cases of this in our model, although we cannot guarantee they do not exist for some combinations of parameter values.

Our model allows for the evolution of niche position, but assumes niche width (σ_a or σ_p) is a fixed character, an assumption which is the basis of the isodiversity plot (Fig. 2). It is of course possible to let niche width evolve as well. By assuming a trade-off between niche width and overall resource uptake, it has been shown that an adaptive radiation of consumers feeding on a distribution of resources is still possible and, depending on the strength of the trade-off, the resulting ESS community will be more or less diverse (Ackermann and Doebeli, 2004). An extension of our model to allow for niche width evolution would be very interesting, but we consider it out of scope here. We merely conclude that previous theoretical work at least does not exclude the possibility of a gradual build-up of a predator–prey community to various levels of biodiversity, even if niche width is not a fixed character.

The convergent stable ESS represents an evolutionary endpoint, but says little about the process to get there. We studied niche co-evolution to examine the gradual build-up of communities to the ESS, starting with one prey and one predator species. The evolutionary dynamics took a given set of species to a convergent stable set of strategies in trait space – the niche archetypes. A niche archetype is the expected outcome of gradual, directional evolution, and is either a local minimum or a local maximum of the adaptive landscape. When a strategy converged on a local minimum, we invoked adaptive speciation or invasion to introduce a new species with a strategy near to the 'parent' strategy. This increases the diversity of the community and leads to additional co-evolution. We let

this combination of strategy dynamics and speciation/invasion continue until either the community had achieved the ESS or until all species resided on local maxima of the adaptive landscape. When stuck at non-ESS local maxima, the only way to continue progress towards the ESS is invasion by a species with a strategy distant from the strategies of the extant species.

Far from the ESS, the community tends to be very unstable, both ecologically and evolutionarily. In such a community, it is relatively easy for a new species to invade. The invasion causes immediate ecological and evolutionary changes in the rest of the community. At the new ecological equilibrium (or the new attractor), a new adaptive landscape unfolds, which has little resemblance to the situation before the invasion. An invading species can in this way open the door to further invasions at trophic levels previously resistant to invasions (Fig. 5). Similarly, an adaptive speciation at one trophic level makes possible further speciations at lower or higher trophic levels.

If, on the other hand, the species at one trophic level fail to speciate, and at the same time are protected from invasions, the whole community can be stuck at pre-ESS niche archetypes. Here we have paid very little attention to details of the speciation process, but theory suggests that adaptive speciation can take a very long time, at least compared with directional evolution (Metz *et al.*, 1996; Bolnick, 2004). Even the first step – the development of a stable (long-lasting) polymorphism – can take a very long time or even be totally prevented in populations subject to strong demographic (Claessen *et al.*, 2007) or environmental (Johansson and Ripa, 2006) stochasticity. Furthermore, in our model the fitness landscape flattens out considerably towards the end of an adaptive radiation and the last few speciations are driven by very weak disruptive selection. We therefore speculate that many communities may very well fail to reach the ESS communities given by the local environment. Instead, one or several species can be stuck at evolutionary branching points (i.e. fitness minima), and the communities will be open to invasions by alien species, even closely related ones (constrained by the same *G*-function). This speculation is supported by the finding that disruptive selection is as common as stabilizing selection in studied natural populations (Kingsolver *et al.*, 2001).

The evolutionary instability of the pre-ESS community makes good intuitive sense, but the trend from unstable ecological dynamics to a stable equilibrium at the ESS is harder to explain. We currently have no deeper understanding of this interesting phenomenon, and leave it for future investigations.

The niche archetypes exist whether or not they are occupied by any extant species. They represent points in strategy trait space where a community is predicted to spend a lot of time, whereas the gradual niche co-evolution between such points is predicted to be relatively fast (Metz *et al.*, 1996). Here, following tradition, we have focused primarily on the ESS community, but speculate on the potential importance of the pre-ESS niche archetypes. Using co-evolutionary models to predict patterns of extant communities, the ESS community works well as a benchmark, an idealized state, but may not be the most likely configuration of species.

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REFERENCES

- Abrams, P.A., Harada, Y. and Matsuda, H. 1993a. On the relationship between quantitative genetic and ESS models. *Evolution*, **47**: 982–985.
- Abrams, P.A., Matsuda, H. and Harada, Y. 1993b. Evolutionarily unstable fitness maxima and stable fitness minima of continuous traits. *Evol. Ecol.*, **7**: 465–487.
- Ackermann, M. and Doebeli, M. 2004. Evolution of niche width and adaptive diversification. *Evolution*, **58**: 2599–2612.
- Bolnick, D.I. 2004. Waiting for sympatric speciation. *Evolution*, **58**: 895–899.
- Brown, J.H., Kelt, D.A. and Fox, B.J. 2002. Assembly rules and competition in desert rodents. *Am. Nat.*, **160**: 815–818.
- Brown, J.S. and Pavlovic, N.B. 1992. Evolution in heterogeneous environments: effects of migration on habitat specialization. *Evol. Ecol.*, **6**: 360–382.
- Brown, J.S. and Vincent, T.L. 1987. Coevolution as an evolutionary game. *Evolution*, **41**: 66–79.
- Brown, J.S. and Vincent, T.L. 1992. Organization of predator–prey communities as an evolutionary game. *Evolution*, **46**: 1269–1283.
- Christiansen, F.B. and Loeschcke, V. 1980. Evolution and intraspecific exploitative competition. 1. One-locus theory for small additive gene effects. *Theor. Pop. Biol.*, **18**: 297–313.
- Claessen, D., Andersson, J., Persson, L. and de Roos, A.M. 2007. Delayed evolutionary branching in small populations. *Evol. Ecol. Res.*, **9**: 51–69.
- Cohen, Y., Vincent, T.L. and Brown, J.S. 1999. A G-function approach to fitness minima, fitness maxima, evolutionarily stable strategies and adaptive landscapes. *Evol. Ecol. Res.*, **1**: 923–942.
- Diamond, J.M. 1975. Assembly of species communities. In *Ecology and Evolution of Communities* (M.L. Cody and J.M. Diamond, eds.), pp. 342–444. Cambridge, MA: Harvard University Press.
- Dieckmann, U. and Doebeli, M. 1999. On the origin of species by sympatric speciation. *Nature*, **400**: 354–357.
- Dieckmann, U. and Law, R. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. *J. Math. Biol.*, **34**: 579–612.
- Eshel, I. and Motro, U. 1981. Kin selection and strong evolutionary stability of mutual help. *Theor. Pop. Biol.*, **19**: 420–433.
- Fletcher, R. 1987. *Practical methods of optimization*, 2nd edn. Chichester: Wiley.
- Geritz, S.A.H., Kisdi, É., Meszéna, G. and Metz, J.A.J. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. *Evol. Ecol.*, **12**: 35–57.
- Heino, M., Metz, J.A.J. and Kaitala, V. 1998. The enigma of frequency-dependent selection. *Trends Ecol. Evol.*, **13**: 367–370.
- Iwasa, Y., Pomiankowski, A. and Nee, S. 1991. The evolution of costly mate preferences II. The ‘handicap’ principle. *Evolution*, **45**: 1431–1442.
- Johansson, J. and Ripa, J. 2006. Will sympatric speciation fail due to stochastic competitive exclusion? *Am. Nat.*, **168**: 572–578.
- Kingsolver, J.G., Hoekstra, H.E., Berrigan, D., Vignieri, S.N., Hill, S.E., Hoang, A. *et al.* 2001. The strength of phenotypic selection in natural populations. *Am. Nat.*, **157**: 245–261.
- Kisdi, É. and Geritz, S.A.H. 2003. Competition–colonization trade-off between perennial plants: exclusion of the rare species, hysteresis effects and the robustness of coexistence under replacement competition. *Evol. Ecol. Res.*, **5**: 529–548.
- MacArthur, R.H. and Levins, R. 1967. The limiting similarity, convergence and divergence of coexisting species. *Am. Nat.*, **101**: 377–385.
- Marrow, P., Dieckmann, U. and Law, R. 1996. Evolutionary dynamics of predator–prey systems: an ecological perspective. *J. Math. Biol.*, **34**: 556–578.

- May, R.M. 1973. *Stability and Complexity in Model Ecosystems*. Princeton, NJ: Princeton University Press.
- Maynard Smith, J. 1966. Sympatric speciation. *Am. Nat.*, **100**: 637–650.
- Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge: Cambridge University Press.
- Metz, J.A.J., Nisbet, R.M. and Geritz, S.A.H. 1992. How should we define ‘fitness’ for general ecological scenarios? *Trends Ecol. Evol.*, **7**: 198–202.
- Metz, J.A.J., Geritz, S.A.H., Meszéna, G., Jacobs, F.J.A. and van Heerwaarden, J.S. 1996. Adaptive dynamics, a geometrical study of the consequences of nearly faithful reproduction. In *Stochastic and Spatial Structures of Dynamical Systems* (S.J. van Strien and S.M. Verduyn Lunel, eds.), pp. 183–231. Amsterdam: North-Holland.
- Morris, D.W. 2003. Toward an ecological synthesis: a case for habitat selection. *Oecologia*, **136**: 1–13.
- Ripa, J. 2009. When is sympatric speciation truly adaptive? An analysis of the joint evolution of resource utilization and assortative mating. *Evol. Ecol.*, **23**: 31–52.
- Rosenzweig, M.L. 1978. Competitive speciation. *Biol. J. Linn. Soc.*, **10**: 275–289.
- Schluter, D. 2001. Ecology and the origin of species. *Trends Ecol. Evol.*, **16**: 372–380.
- Vincent, T.L. and Brown, J.S. 1986. Evolution under nonequilibrium dynamics. In *Mathematical Modelling in Science and Technology, Proceedings of the Fifth ICMM* (X.J.R. Avula, G. Leitman, C.D. Mote, Jr. and E.Y. Rodin, eds.). New York: Pergamon Press.
- Vincent, T.L. and Brown, J.S. 1988. The evolution of ESS theory. *Annu. Rev. Ecol. Syst.*, **19**: 423–443.
- Vincent, T.L. and Brown, J.S. 2005. *Evolutionary Game Theory, Natural Selection, and Darwinian Dynamics*. Cambridge: Cambridge University Press.
- Vincent, T.L., Cohen, Y. and Brown, J.S. 1993. Evolution via strategy dynamics. *Theor. Pop. Biol.*, **44**: 149–176.

APPENDIX: NUMERICAL CONVERGENCE STABILITY ANALYSIS

As described in the main text, we simulated a system of 501 prey and 501 predator populations with u - and v -values evenly spaced between -5 and $+5$. In essence, we simulated the dynamics of a distribution of prey and predator densities along the u - and v -axes. Eventually, usually after a few thousand iterations, clearly identifiable distribution peaks developed, which we interpreted as a possible ESS solution. A distribution peak was defined as a population with higher density than its two neighbour populations. If there were as many distribution peaks as peaks in the corresponding fitness landscape, further testing was carried out. We extracted the peak populations into a candidate ESS community. The populations of the extracted community were, however, no longer in ecological or evolutionary equilibrium. First, ecological equilibrium was re-established by iterating equations (8) and (9) until the absolute log fitness of all populations was smaller than 10^{-10} [if possible, this process was speeded up using a Newton-Raphson technique (Fletcher, 1987)]. Second, the u - and v -strategies of this community were adjusted somewhat to find a more exact stationary point of the adaptive dynamics (i.e. where all fitness gradients were zero). This was done using the Jacobian matrix of the adaptive dynamics (see below) and small Newton-Raphson steps (1/10 of a full step) (cf. Fletcher, 1987). Ecological equilibrium was re-established as above after each step. We stopped the adjustment when all fitness gradients were smaller than 10^{-6} in absolute value. At this point, the eigenvalues of the Jacobian of the adaptive dynamics were calculated numerically, as well as the second derivative of the G -functions (equations 3 and 4). If all eigenvalues had negative real parts and all second

derivatives were negative, the community was classified as a convergent stable ESS. All communities represented in Fig. 2 have this property.

The Jacobian of the adaptive dynamics was calculated by numerical differentiation of the fitness gradients, which evaluate to:

$$g_{N,i}(\mathbf{u}, \mathbf{v}) = \left. \frac{\partial G_1(u, \mathbf{u}, \mathbf{v}, \mathbf{N}^*, \mathbf{P}^*)}{\partial u} \right|_{u=u_i} = \frac{r}{K(u_i)} \sum_{k=1}^m a(u_i, u_k) N_k^* \left(\frac{u_i - u_k}{\sigma_a^2} - \frac{u_i}{\sigma_K^2} \right) + \sum_{j=1}^n \frac{u_i - v_j}{\sigma_p^2} b(u_i, v_j) P_j^*$$

for the prey and

$$g_{P,j}(\mathbf{u}, \mathbf{v}) = \left. \frac{\partial G_2(v, \mathbf{u}, \mathbf{v}, \mathbf{N}^*, \mathbf{P}^*)}{\partial v} \right|_{v=v_j} = \sum_{i=1}^m \frac{u_i - v_j}{\sigma_p^2} b(u_i, v_j) N_i^*$$

for the predators. The total gradient vector consists of the fitness gradients of all populations:

$$\mathbf{g} = (g_{N,1}, g_{N,2}, \dots, g_{N,m}, g_{P,1}, g_{P,2}, \dots, g_{P,n})^T$$

If it can be assumed that the evolutionary dynamics are proportional to population size and the fitness gradient (equations 10 and 11), the Jacobian of these dynamics will determine the convergent stability of a candidate ESS community. Each element of the Jacobian was calculated by numerical differentiation as

$$J_{kl} = \delta_k N_k \frac{g_k(u_l = u_l^* + \Delta) - g_k(u_l = u_l^* - \Delta)}{2\Delta}, \quad k, l = 1, \dots, (m+n)$$

(or the equivalent for a predator strategy v_l), where Δ was set to 10^{-7} . Each change Δ of a single u - or v -value was accompanied by re-establishment of ecological equilibrium, as above.

