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Evolutionary responses of communities to extinctions

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Evolutionary responses of communities to extinctions

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ABSTRACT

Question: What are the evolutionary consequences of extinctions in ecological communities? Can evolution restore pre-extinction communities by replacing lost ecological strategies with similar ones, or will communities change in fundamental ways and never be the same again?

Mathematical approach: We develop and explore a new framework based on evolutionary domains of attraction (EDAs), defined as sets of strategy combinations from which a particular ESS community can be attained through gradual evolution. The latter dynamics may include three types of evolutionary processes: continuous strategy adaptation in response to directional selection, evolutionary branching in response to disruptive selection, and evolutionarily driven extinction.

Key assumptions: We consider gradual frequency-dependent evolution in ecological communities, with evolutionary dynamics being fully determined by the strategy composition of a community's resident species.

Results: The EDA approach distinguishes ESS communities that gradual evolution can restore after extinctions from ESS communities for which this option does not exist or is constrained. The EDA approach also offers a natural definition of 'evolutionary keystone species' as species whose removal causes a community to shift from one EDA to another. Our study highlights that environmentally driven extinctions can readily cause such shifts. We explain why the evolutionary attainability of an ESS community through gradual evolution from a single precursor species does not imply its evolutionary restorability after extinctions. This shows that evolution driven by frequency-dependent selection may lead to Humpty-Dumpty effects and community closure on an evolutionary time scale. By establishing EDAs for several example food webs, we discover that evolutionarily driven extinctions may be crucially involved in the evolutionary restoration of ESS communities.

INTRODUCTION

Extinctions can have far-reaching ecological and evolutionary repercussions. On short time scales, removal of a single species may cause extinction cascades and restructure ecological communities (Paine, 1966; Simberloff, 2003; Wootton and Downing, 2003). On long time scales, extinctions may create new evolutionary opportunities and reshape adaptive landscapes via the differential survivorship of species (Vermeij, 1987; Jablonski, 1989; McKinney, 1997). At the same time, many extinctions take place without noticeable effects on ecological communities and without leaving deep traces in fossil records (Purvis *et al.*, 2000; Erwin, 2001). Understanding which mechanisms underlie these different outcomes of extinctions is critical for important objectives as diverse as interpreting fossil patterns (Raup, 1994) and predicting the long-term consequences of the current biodiversity crisis (Myers and Knoll, 2001).

In this study we investigate the evolutionary implications of extinctions for community structures. Inevitably, the disappearance of a species changes the biotic environment for the species remaining in a community. These are therefore likely to experience altered selection pressures, which in turn can drive gradual evolutionary changes. Such evolution may have a range of different outcomes. One possibility is character release (Grant, 1972) and the adaptive adjustments of niche positions, including parallel shifts, convergence, and divergence (Abrams, 1996). Models focusing on the reverse phenomenon, species introduction into communities, have shed light on the coevolutionary mechanisms involved in such shifts (Slatkin, 1980; Rummel and Roughgarden, 1983; Taper and Case, 1985; Abrams, 1986; Drossel and McKane, 1999). Another, more malignant, outcome of gradual evolution is extinction. Extinction driven by natural selection readily occurs in models describing a wide range of ecological settings. Frequency-dependent evolution within a single species can cause sudden population collapses (evolutionary suicide; Ferrière, 2000; Gyllenberg and Parvinen, 2001; Parvinen, 2005). A species can also undergo a gradual decline to critically small population sizes, either again driven by intraspecific evolution (evolutionary deterioration; Matsuda and Abrams, 1994; Dieckmann and Ferrière, 2004) or by evolution in coexisting species (coevolutionary extinction; Rummel and Roughgarden, 1983). Brown and Vincent (1992) put forward models in which the removal of predators, termed ‘evolutionary keystones,’ caused evolutionary convergence in the niche positions of their prey, resulting in competitive exclusions. Their study illustrates how the extinction of a species can trigger further, evolutionarily driven, extinctions. Similar coevolutionary extinction cascades were found by Bronstein *et al.* (2004) in models of mutualism.

A related, but less explored, possibility is that gradual evolution activated by extinctions leads to diversification. The capacity of ecological interactions to drive diversification is increasingly emphasized in the literature (Bush, 1975; Schluter, 1994; Rainey and Travisano, 1998; Travisano and Rainey, 2000; Dieckmann and Ferrière, 2004; Grant and Grant, 2006). In particular, it is theoretically well established that frequency-dependent selection can cause evolution towards fitness minima (Rosenzweig, 1978; Metz *et al.*, 1992; Abrams *et al.*, 1993; Cohen *et al.*, 1999). The ensuing disruptive selection can split up lineages through a process known as evolutionary branching (Metz *et al.*, 1996; Geritz *et al.*, 1998). Evolutionary branching is a form of gradual evolution that may give rise to coalitions of stably coexisting ecological strategies (e.g., Geritz *et al.*, 1999; Egas *et al.*, 2004). Subsequent evolution may then lead to further evolutionary branching. In this manner, recursive

evolutionary branching can originate whole ecological communities through adaptive radiations (e.g., Loeuille and Loreau, 2004; Ito and Ikegami, 2006; Ito *et al.*, 2009).

That gradual evolution can thus endogenously generate diversity draws attention to the possibility that species that are lost from a community through extinction may be replaced with phenotypically equivalent ones through post-extinction diversification. Communities may or may not undergo such evolutionary restoration after extinctions, and even when it happens, the restoration may be either full or only partial. However, under which circumstances these different outcomes are expected is not clear, for two reasons. First, the typical ecological scenario envisioned in most models of evolutionary branching is not representative of the diversification processes expected in post-extinction communities. For example, studies of evolutionary branching commonly focus on diversification starting from a single species residing in an empty niche space. By contrast, in post-extinction communities, the pace and eventual level of diversification will naturally be contingent on the species that remain in the community. Compared to the "virgin scenario" in an empty niche space, evolutionary branching may be helped or hampered in these partly occupied ecological environments.

Second, established concepts for classifying the stability of evolutionary processes do not offer the guidance necessary for predicting whether, and if so to what extent, a community is evolutionarily restorable. Classical evolutionary game theory assumes that the outcome of evolution is an evolutionarily stable strategy (ESS), a phenotype that is unbeatable by any variant phenotype (Maynard Smith, 1976). However, taking into account that adaptive evolution typically proceeds gradually, through changes with small phenotypic effect, the ESS condition itself is of but limited relevance for understanding and predicting the dynamical processes underlying evolutionary restoration. First of all, evolution may become stuck at a local fitness maximum. Moreover, if selection is frequency-dependent, an unbeatable strategy may not be convergence stable, i.e., attainable through gradual evolution from nearby phenotypes (Eshel and Motro, 1981). In fact, Eshel and Motro (1981) showed that evolutionary stability and convergence stability are independent properties, which therefore can occur in any combination. It has thus been suggested that endpoints of the evolutionary process need to possess both properties, evolutionary stability and convergence stability. This requirement defines so-called continuously stable strategies (CSSs), which can also be generalized to multispecies scenarios (Vincent *et al.*, 1996). Crucially, however, continuous stability is not sufficient for evolutionary restorability. Since convergence stability is a local property, it is possible that gradual evolution following extinction leads away from a CSS and eventually converges on a different evolutionary attractor. At a more fundamental level, it is not even clear how the concept of convergence stability can be defined when species numbers may be changing, such as during evolutionary restoration.

In this study we introduce evolutionary domains of attraction (EDAs) as a tool for mapping out the possible evolutionary pathways from post-extinction communities to evolutionary attractors. We focus on pathways characterized by gradual evolution, which may variously include continuous strategy adaptations in response to directional selection, evolutionary branching of strategies in response to disruptive selection, and evolutionary extinctions of strategies as outlined above. We show how the EDA approach can help characterize the evolutionary attainability and restorability of ESS communities. We also apply the EDA approach to study possible alternative routes to ESSs and evolutionary consequences of extinctions in two specific food-web models. Although the food webs contain only two evolving consumer species with one-dimensional strategies, the EDA approach reveals surprisingly rich evolutionary dynamics in these systems.

Two important phenomena may interfere with the restoration of a community through endogenous evolution. To start with, vacant niches left by extinct species may be filled through immigration events. Such events are, by definition, exogenous to the system under consideration, which will usually complicate predicting their effects. Next, although disruptive selection inevitably arises at evolutionary branching points, it may still not lead to the splitting of lineages. Requirements for speciation to occur in sexually reproducing populations remain a topic of active research (e.g., Dieckmann *et al.*, 2004; Gavrilets, 2005). Furthermore, stochastic effects may delay or impede evolutionary branching, even in asexual populations (Johansson and Ripa, 2006; Claessen *et al.*, 2007). The EDA approach we introduce below focuses on predicting the eventual outcome of gradual evolution in the absence of immigration events and speciation obstacles. The latter are readily incorporated into the EDA approach by analyzing jumps in strategy space and by examining traps at evolutionary branching points, respectively.

This article is structured as follows. First we introduce the EDA approach and explain how it can be used to study evolutionary attainability and restorability. Then we explain how to identify and use EDAs in two example models. We then compare predictions of the EDA approach with results from (mostly theoretical) studies of invasion-structured communities. We conclude by discussing our results in relation with two fundamental kinds of diversification processes; adaptive radiation within local communities and large-scale evolutionary restoration processes following mass extinctions.

EVOLUTIONARY DOMAINS OF ATTRACTION

Gradual evolution

The EDA approach developed here is based on assumptions commonly made when studying gradual evolution through quantitative genetics (Lande, 1976; Iwasa *et al.*, 1991; Abrams *et al.*, 1993), strategy dynamics (Vincent *et al.*, 1993), and adaptive dynamics (Dieckmann and Law, 1996; Metz *et al.*, 1996; Geritz *et al.*, 1998). We assume that the ecological strategy of a species is characterized by a quantitative trait. We let z_i denote the trait value and N_i the population size of a species i. Trait values of a community of species $i = 1,...,n$ are thus described by the vector $\mathbf{z}$ that contains the trait values $z_1,...,z_n$. We denote by $w(z', \mathbf{z})$ the fitness of an individual with trait value z' in a community with trait values $\mathbf{z}$. To keep the notation simple, we focus on situations with a shared trait space and one trait per species, but our approach readily generalizes to several trait spaces and several traits per species. Below we discuss the three elements of gradual evolution, by describing in turn the continuous adaptation, evolutionary branching, and evolutionary extinction of strategies.

Continuous adaptation of strategies. We assume that the trait values in $\mathbf{z}$ evolve according to

$$\frac{d}{dt}\mathbf{z} = \mathbf{C}(\mathbf{z})\mathbf{g}(\mathbf{z}), \qquad (1)$$

where $\mathbf{g}(\mathbf{z})$ is a vector describing the selection gradient and $\mathbf{C}(\mathbf{z})$ is a matrix describing how the selection gradient translates into evolutionary rates. The ith element of $\mathbf{g}(\mathbf{z})$ thus describes the directional selection pressure on the trait of species i, $g_i(\mathbf{z}) = \partial w(z', \mathbf{z}) / \partial z'\big|_{z'=z_i}$.

This form of evolutionary dynamics is very general, and naturally arises in quantitative genetics (Lande, 1976; Iwasa *et al.*, 1991), strategy dynamics (Vincent *et al.*, 1993), and adaptive dynamics (Dieckmann and Law, 1996). Equation 1 thus represents different evolutionary scenarios depending on the interpretation and form of $\mathbf{g}$ and $\mathbf{C}$. For example, the elements of $\mathbf{g}$ may describe frequency-independent selection on a fixed fitness landscape (Lande, 1976) or frequency-dependent selection derived from underlying ecological models (Abrams *et al.*, 1993; Vincent *et al.*, 1993; Dieckmann and Law, 1996). In one interpretation, equation 1 can describe evolution in communities with standing genetic variation, as in quantitative genetics (Lande, 1976; Iwasa *et al.*, 1991; Abrams *et al.*, 1993) or strategy dynamics (Vincent *et al.*, 1993). Then $\mathbf{g}$ describes the selection pressures on mean trait values and $\mathbf{C}$ is the diagonal matrix of population-level additive genetic variances. The latter may be assumed to be constant (Lande, 1976), to change as a fixed function of a species' mean trait values (Abrams *et al.*, 1993), or to follow their own selection-driven dynamics (Vincent *et al.*, 1993). In another interpretation, equation 1 can describe the mutation-limited evolution of (nearly) monomorphic populations, as in adaptive dynamics theory. Then $\mathbf{g}$ describes the selection pressures on resident trait values and $\mathbf{C}$ is the diagonal matrix with elements that are proportional to the product of mutation probabilities, mutation variances, and the equilibrium population sizes of resident populations (Dieckmann and Law, 1996). The latter three factors may all be functions of trait values. When Equation 1 is generalized to multiple traits per species, $\mathbf{C}$ assumes a block-diagonal structure, with the off-diagonal elements in each species' block describing additive genetic or mutational covariances among that species' traits (Lande, 1979; Falconer and Mackay, 1996; Leimar, 2001).

Continuous strategy adaptations will proceed according to equation 1 until a species goes extinct or until the evolving community reaches an evolutionarily singular strategy $\mathbf{z}^*$, defined by a vanishing selection gradient $\mathbf{g}(\mathbf{z}^*) = 0$ and thus by the absence of directional selection pressures (Metz *et al.*, 1996; Geritz *et al.*, 1998). What may happen at $\mathbf{z}^*$ can be evaluated by studying the shape of the local fitness landscape. If $\partial^2 w(z', \mathbf{z}^*) / \partial z'^2 \big|_{z'=z_i} < 0$ for all i, $\mathbf{z}^*$ is an ESS. Since $\mathbf{z}^*$ was reached through gradual evolution, it classifies as a CSS as well. The inequality ensures that the trait values of each species are situated at a fitness maximum, so that all selection pressures are stabilizing and the community's evolution therefore stops.

Evolutionary branching of strategies. When the last inequality is reversed for a species i, that species experiences disruptive selection. This may result in evolutionary branching, i.e., in the splitting of lineages by frequency-dependent disruptive selection (Metz *et al.*, 1996; Geritz *et al.*, 1998). After such an evolutionary branching, the number n of strategies is incremented by 1, and the new trait is added to $\mathbf{z}$ (with an initial value corresponding to the ancestral trait).

Evolutionary extinction of strategies. The evolutionary extinction of species i results when its equilibrium population size goes to zero due to evolution in $\mathbf{z}$ (Geritz *et al.*, 1999; Dercole, 2003; Dieckmann and Ferrière, 2004). After such an evolutionary extinction, the number n of strategies is decremented by 1, and the lost trait is removed from $\mathbf{z}$.

It is important to distinguish evolutionary extinctions from those driven by systematic environmental changes (pulse and press perturbations; Bender *et al.*, 1984). The former occur due to causes that are internal to the evolving community, whereas the latter are driven externally. While an environmental change may do more than cause the loss of one or more species from a community, our analyses of the evolutionary consequences of extinctions focus on the effects of these extinctions alone, in close correspondence with studies of the ecological consequences of extinctions (e.g., Borrvall *et al.*, 2000; Lundberg *et al.*, 2000).

Definition of evolutionary domains of attraction

We define the evolutionary domain of attraction (EDA) of an ESS as the set of all strategy combinations from which the ESS is attainable through gradual evolution.

By combining the continuous adaptation of strategies with increases (through evolutionary branching) and decreases (through evolutionary extinction) in the number of strategies, the definition of EDAs fundamentally goes beyond the simpler concept of domain (or basin) of attraction widely used in the general context of dynamical systems. The latter has previously been applied to evolutionary dynamics restricted to the continuous adaptation of strategies (e.g., Dieckmann and Law, 1996; Law *et al.*, 1997; Geritz *et al.*, 1999; Kisdi and Geritz, 1999; Dercole, 2003; HilleRisLambers and Dieckmann, 2003; Le Galliard *et al.*, 2003; Magori *et al.*, 2003).

Graphical representation of evolutionary domains of attraction

One advantage of EDAs is that they can easily be studied and understood graphically. Here we describe how. To keep illustrations simple, we start with focusing on two-species communities, whose dimorphic ESSs are embedded in two-dimensional trait spaces. The graphical representation of EDAs in three-species communities will be discussed later, in connection with Figure 5.

Figure 1 illustrates the EDA of a hypothetical dimorphic ESS that can be reached through evolutionary branching. The trait spaces and evolution of a single species (monomorphic dynamics) and of two coevolving species (dimorphic dynamics) are depicted here in a single figure, with the single-species dynamics occurring along the diagonal ($z_1 = z_2$), which we hereafter thus call the monomorphic diagonal. In Figure 1A, a single species will evolve towards the branching point (filled square) if its trait value is situated within the interval (thick dark-gray line) of the monomorphic diagonal that belongs to the EDA (dark-gray region, including that line). At the branching point, the species may split into two species, which in turn will evolve in different directions away from each other and thereby leave the diagonal ($z_1 \neq z_2$, point a in Fig. 1A). The two coevolving species will reach the ESS (filled circle) where selection on both species is stabilizing and hence evolution stops (point b in Fig. 1A). If the community initially contained two species with different traits, such that their trait-value combination (i.e., the corresponding point in the two-dimensional trait space outside the monomorphic diagonal) was situated within the EDA, the dimorphic ESS would also be attained (point c in Fig. 1A).

For species to coevolve within an EDA, they must be able to coexist: therefore, an EDA is always a subset of the domain of coexistence (light-gray region). The latter is defined according to a suitable criterion such as mutual invasibility. Since the labeling of species by subscripts 1 and 2 is arbitrary, EDAs and coexistence domains are always invariant under mirroring alone the monomorphic diagonal. For the sake of simplicity, these redundant mirror images are not shown in Figure 1, nor in the following figures.

Figure 1A is an example of how to depict gradual evolution on a changing adaptive landscape in a compact and economic way. Each single point in the one- and two-dimensional trait spaces of this figure corresponds to a unique adaptive landscape. The direction and speed of evolution at any such point depend on the local slopes of the adaptive landscape. Likewise, when directional selection is absent, the stabilizing or disruptive nature of selection depends on the local curvatures of the adaptive landscape. This is illustrated in Figure 1B for dimorphic coalitions with trait-value combinations corresponding to the points a, b, and c in Figure 1A. These adaptive landscapes not only affect the direction

and speed of evolution for the two shown resident species, but they also reveal which other trait values are able to invade the community by immigration: such immigrants need to experience positive fitness values at unoccupied trait values away from the resident species. It must be kept in mind, however, that whether such immigrants can eventually coexist with the resident species is a different question that needs to be addressed in terms of the coexistence domain.

We can therefore conclude that burdening the graphical representation by keeping track of all possible adaptive landscapes would be unnecessarily complicated for our purposes, for two reasons. First, the graphical representation illustrated in Figure 1 provides all information necessary for understanding gradual evolution: directional selection on resident species is depicted by the direction and length of arrows, while the occurrence of stabilizing and disruptive selection is indicated by the labeling of evolutionarily singular points. Second, the graphical representation illustrated in Figure 1 also provides key information for understanding invasions through immigration: the coexistence domain shows, for any one resident species, which other trait values could immigrate and coexist.

In addition, the graphical representation illustrated in Figure 1 also provides all information necessary for understanding extinctions: these are represented as projections from an n-dimensional trait space to an $(n-1)$-dimensional trait space. As mentioned above, in this study we consider both environmentally driven extinctions and evolutionarily driven extinctions. Figure 1 illustrates both types. The environmentally driven extinction of species 1 at the dimorphic ESS is shown as a projection (horizontal dotted arrow) from the ESS to the point on the monomorphic diagonal corresponding to the trait value of the remaining species 2. An evolutionarily driven extinction occurs where the trajectories of gradual evolution leave a coexistence domain., It is thus useful to highlight in the graphical representation those parts of the border of this domain that attract evolutionary trajectories instead of repelling them. In Figure 1, the evolutionarily driven extinction of species 2 at the attracting part of the coexistence-domain border (thick continuous curve) is shown as a projection (vertical dotted arrow) from this border to the point on the monomorphic diagonal corresponding to the trait value of the remaining species 1. Notice that, because of the repellor (open circle) situated on the monomorphic diagonal, the branching point, and thus the dimorphic ESS, can no longer be reached after this evolutionary extinction.

Classification of evolutionary attainability and restorability based on evolutionary domains of attraction

We will now use the EDA approach introduced above to characterize the evolutionary attainability and restorability of dimorphic ESSs. Figure 2 introduces the classification of five qualitatively different cases.

Figure 2A shows an ESS that lacks an EDA. Even though the ESS is uninvadable, it is not convergence stable and therefore impossible to reach through continuous adaptation. When such ESSs are nevertheless surrounded by a coexistence domain, they are known as Garden-of-Eden configurations (Hofbauer and Sigmund, 1990; Nowak, 1990). In Figure 2B, the ESS has an EDA. It may therefore be reached through the continuous adaptation of nearby strategies, which makes it a CSS. However, since the monomorphic diagonal is not included in the EDA, this CSS cannot be attained through gradual evolution of a single precursor species. In Figures 2C, 2D, and 2E, the ESSs are also attainable from a single precursor species, through the combination of evolutionary branching and continuous adaptation. These three cases, however, differ in the extent to which the CSS may be restored after an extinction. If the species that remains after the extinction is situated within the EDA of the

original CSS, it will evolve to the branching point and may thus give rise to two new species that eventually will evolve to the original CSS. Figure 2C shows a CSS that cannot be restored in this way, since both extinction projections fall outside the EDA. Figure 2D shows a partially restorable case, where the CSS can be restored after extinction of one of the two species (species 1), but not after extinction of the other one (species 2). Figure 2E, finally, shows a fully restorable CSS, where both extinction projections fall into the EDA of the original CSS.

Based on these observations, we can introduce the following general classification of ESSs. All ESSs are uninvadable, but differ in their degree of attainability and restorability. If they are surrounded by an EDA, they are locally attainable, and thus CSSs. If their EDA includes the monomorphic diagonal, they are attainable from a single precursor species. Yet, they may or may not be restorable. Evolutionary restorability comes in two versions: a CSS may either be restorable after some extinctions only (if some, but not all, extinction projections fall into its EDA), or after all possible extinctions (if all extinction projections fall into its EDA). In the following we will refer to these cases as partially restorable and fully restorable ESSs, respectively.

ATTAINABILITY AND RESTORABILITY IN MODEL FOOD WEBS

We now apply the EDA approach to study attainability and restorability in two specific food-web models. We start with the well-studied scenario of evolving consumer species feeding on two basal resource species (Egas *et al.*, 2004; Ravigné *et al.*, 2004; Diekmann *et al.*, 2005; Rueffler *et al.*, 2006; Ripa, 2009) and show that it may exhibit all the different classes of ESS shown in Figure 2. In this first scenario, the EDA approach also reveals new, more complex routes to ESSs than had previously been reported. We then study a second scenario with a qualitatively different and more intricate food-web structure. In this second scenario, a predator species may specialize either on a basal resource or on a non-evolving consumer species. Applying the EDA approach to the second scenario shows that community restoration can involve evolutionarily driven extinctions and may critically depend on processes other than gradual evolution, such as the reinvasion of excluded species. The second example also illustrates how evolutionary restoration may take very different pathways depending on the species that goes extinct.

In the models used as examples below, the efficiency of attacking one of the prey is assumed to trade off against the efficiency of attacking the other, a widely used tenet of consumer-resource ecology (HilleRisLambers and Dieckmann, 2003; Egas *et al.*, 2004; Abrams, 2006). The evolving consumers are characterized by a single quantitative trait z that can take values in the interval $[0,1]$. The trade-off arises from letting z represent the fractional investment into attacking prey 1 and letting $1-z$ represent the fractional investment into attacking prey 2. The corresponding attack rates $\alpha(z)$ and $\alpha(1-z)$ are then functions of these fractional investments, with α denoting a monotonically increasing function and $\alpha(0)=0$. The strength of the trade-off is controlled by a parameter s (Fig. 3A). When $s=1$, the trade-off between the two attack rates is linear; it becomes stronger (weaker) for higher (lower) values of s. More information about the function α is presented in Appendix A. Functional responses of consumers are linear and basal resources follow logistic growth. Trait values are assumed to evolve according to the canonical equation of adaptive dynamics (Dieckmann and Law, 1996). More information about the ecological and evolutionary dynamics is presented in Appendix B.

Example 1: Evolving consumers feeding on two resources

Figure 3 shows EDAs of the ESSs of two coevolving consumers, with attainability and restorability properties corresponding to the classification in Figure 2. For an extremely strong trade-off (attack rate $\alpha(z)=1$ if $z=1$ and $\alpha(z)=0$ otherwise), only the two pure specialists ($z_1=1$, $z_2=0$) are viable (point c in Fig. 3C), resulting in an ESS without an EDA (as in Fig. 2A). Notice, however, that this requires a discontinuous mapping from traits to attack rates, since a continuous mapping would render viable trait values very close to 0 or 1. Using the trade-off function in Figure 3A, we obtain dimorphic ESSs that are all attainable (and hence are CSSs). Trade-off strength s decreases when we go from D over E to F. In Figure 3D, the CSS is attainable from certain dimorphic coalitions, but not through evolutionary branching at the monomorphic diagonal (as in Fig. 2B). In Figure 3E, the monomorphic diagonal is included in the EDA, but extinction projections from the dimorphic CSS are not. The dimorphic CSS is hence attainable from a single precursor species, but it is not restorable (as in Fig. 2C). A fully restorable case (as in Fig. 2E) is obtained when s slightly exceeds 1, as shown in Figure 3F. In this case, the whole coexistence domain and the whole monomorphic diagonal belong to a single EDA. After any extinction, the remaining species may therefore evolve back to the branching point and restore the dimorphic CSS. A partially restorable case (as in Fig. 2D) is obtained for asymmetric resource abundances, e.g., when density regulation by the two resource species is of unequal strength (not shown). The EDA of the dimorphic ESS then is a hybrid between the non-restorable case (Fig. 3E) and the fully restorable case (Fig. 3F). Accordingly, the community could be restored after extinction of one species, but not after extinction of the other.

The EDA approach also sheds light on the possible evolutionary routes toward ESSs. Close to the interior border of the coexistence domain in Figure 3D, there are trait-value combinations from which one of the two species will evolutionarily be driven to extinction. In these regions, the low population density of that species will naturally reduce its evolutionary rate. The directions of evolution in these regions are therefore close to vertical or horizontal, and evolutionary extinctions occur when the faster-evolving species forces the community to leave the coexistence domain. After such an extinction, the remaining species will evolve to become a specialist, and thus move toward one of the points a in Fig. 3D. The parts of the coexistence region from which this occurs (light-gray region in Fig. 3D) therefore belong to the EDA of the monomorphic CSSs a, but not to the EDA of the dimorphic CSS c.

In Figure 3E, the monomorphic diagonal contains one branching point (at $z=1/2$) and two repellors situated symmetrically around it. Close to these repellors, there are regions in which one of the species will evolutionarily be driven to extinction, as described above. After such an extinction, the remaining species will evolve either to become a specialist (if extinction occurs in the light-gray region) or to the branching point b (if extinction occurs in the dark-gray region). From the branching point, the dimorphic CSS can be restored. The road of restoration of this dimorphic CSS may hence include continuous adaptation forcing the evolutionary extinction of one species, continuous adaptation of the remaining single species, evolutionary branching, and finally continuous dimorphic divergence until the CSS is reached.

Example 2: Evolving predators feeding on two trophic levels

In our second scenario, one or two evolving predators feed either on a basal resource or on a non-evolving consumer of another resource. Figure 4A shows all resultant possible food-

web configurations (a to f) and summarizes the transitions between them. Figure 4B shows EDAs for the predator trait values and how these correspond to the various possible food-web configurations. A single predator specialized on one resource species (a in Fig. 4) will evolve to the branching point (b in Fig. 4). There it can split into two species, one evolving towards specializing on that resource and another specializing on the non-evolving consumer (c in Fig. 4).

According to the classification scheme above, the food-web configuration c is partially restorable (as in Fig. 2D), since one of the extinction projections falls into its EDA, while the other one falls outside of it. Specifically, extinction of the top predator (species 2 in Fig. 4), which is specialized on feeding on the non-evolving consumer, will change the community into configuration a in Figure 4. From there, the remaining predator will evolve to the branching point b and restore the second predator after divergent adaptation. On the other hand, if the resource specialist (species 1 in Fig. 4) goes extinct, the community will enter the EDA of an alternative evolutionary attractor. Immediately after this extinction, the community is in configuration d. Even if specialized on feeding on the non-evolving consumer, the remaining top predator still has the capacity to evolve toward feeding on the basal resource. Due to the relatively high abundance of the now unused basal resource, the predator will evolve along the monomorphic diagonal towards higher values of z. While increasing its efficiency of feeding on the abundant basal resource, it will itself increase in population density. Even if it becomes a slightly less efficient predator of the non-evolving consumer, the increased density of this predator will exert such a large negative toll on the non-evolving consumer that the latter will go extinct (transition from point e to e' in Fig. 4). The top predator will then continue to specialize on the basal resource, finally reaching configuration f. The community has now been altered in an irreversible way: a new top predator, corresponding to species 2 in configuration c, can neither re-evolve nor reinvade.

If the non-evolving consumer may reinvade through occasional immigration from outside the community, the dimorphic CSS at configuration c would become restorable. After extinction of species 2, the non-evolving consumer would still be driven to extinction as described above. It would be unable to reinvade until the single evolving predator has become mostly specialized on the basal resource (around configuration f, with z close to 1). After invasion of the non-evolving consumer (within the interval of the monomorphic diagonal marked with a black outline in Fig. 4B), the community will be situated within the EDA of the dimorphic CSS. In fact, under these conditions the EDA of the dimorphic CSS will include the EDA of configuration f, so that full restorability of the dimorphic CSS follows.

The two possible evolutionary restoration processes outlined above are qualitatively quite different. After extinction of the top predator, the remaining consumer has a relatively short path to the branching point from which the dimorphic CSS can be restored (a-b-c in Fig. 4). If the non-evolving consumer goes extinct, however, the restoration path becomes much longer and involves a secondary extinction and a necessary reinvasion (d-e-e'-f-a-b-c in Fig. 4).

DISCUSSION

In this study we have shown how evolutionary domains of attraction (EDAs) can be defined and applied to characterize the evolutionary attainability and restorability of ecological communities. The EDA approach helps understand why evolutionary attainability does not imply evolutionary restorability: even if a community of species may be attained through successive evolutionary branching from a single precursor species, gradual evolution after

extinction may not be able to connect to such an evolutionary pathway, and may therefore be prevented from evolutionarily restoring the original community. The EDA approach has also allowed us to highlight the diversity of long-term implications of extinctions in dimorphic ESS communities. In the examples studied, the frequency-dependent selection pressures governing the evolutionary dynamics arise from ecological interactions. The richness of evolutionary pathways and outcomes, and the fact that these can be found even in simple model food webs, underscore that ecological interactions among species play a key role in shaping community evolution in the wake of extinctions.

Generalizations of the EDA approach

While our illustrations above have focused on applying the EDA approach to studying the attainability and restorability of dimorphic ESSs, the concepts, definitions, and methods we have introduced here are readily applicable to communities with more than two species and with more than one trait per species. As an example, Figure 5 provides a schematic illustration of a fully restorable trimorphic CSS. The only complication is that conditions for evolutionary branching in higher-dimensional trait spaces are slightly more complicated than in one-dimensional trait spaces (since the mutual invasibility of incipient branches has to be checked separately, no longer being simply implied by convergence stability and the absence of local evolutionary stability). Naturally, the species coevolving in a community also need not share the same trait spaces and fitness functions. The restorability of species through evolutionary branching will then of course be confined to subsets of species that do share trait spaces and fitness functions. Finally, also non-equilibrium evolutionary attractors, such as evolutionary limit cycles (Dieckmann *et al.*, 1995; Dercole *et al.*, 2006) and chaotic evolutionary attractors (Dercole and Rinaldi, 2008) can be subjected to the EDA approach.

Immigration events and speciation obstacles

As indicated above, immigration events and speciation obstacles can be accounted for in the EDA approach. Specifically, immigration can be seen as a transition from an n-dimensional trait space to an $(n+1)$-dimensional trait space and can thus be represented as a jump of a community's n-dimensional trait combination to the corresponding point defined by the n old and the 1 new trait values. Branching points that are subject to speciation obstacles will be endpoints of evolutionary trajectories, and can be treated as such. Evolutionary restoration can thus be facilitated by immigration, but may be impeded by speciation obstacles. As a trivial example, all ESSs in Figure 2 can be reached directly through the immigration of immigrants with traits corresponding to the ESS trait values, but none of these ESSs can be reached from a single precursor species without evolutionary branching. When evolutionary branching is precluded and potential immigrants do not possess trait values corresponding to ESS values, the EDA approach can be used to study routes to ESSs that result from continuous adaptation in conjunction with immigration events (Rummel and Roughgarden, 1983).

Limitations of the EDA approach

The EDA approach builds upon commonly used models of continuous adaptation in quantitative traits and therefore naturally shares their limitations. An assumption underlying these models is that temporal fluctuations and spatial heterogeneity do not crucially affect the evolutionary dynamics. Ecological variables and functions can then be defined through averages in time (e.g., interaction strengths) and space (e.g., population densities). Deviations

from EDA predictions that are based on averaging temporal fluctuations can be expected to increase with the strength of these fluctuations and with the biological nonlinearities through which they are filtered. As long as stochastic temporal fluctuations do not overwhelm the underlying deterministic dynamics, it is possible to incorporate them into an extended, probabilistic EDA approach by assigning probabilities to each point in trait space that describe how likely various ESSs are attained through gradual evolution (in the simpler, deterministic EDA approach, these probabilities course always equal either 0 or 1). Studying the likelihood for reaching different ESSs in this way is an interesting topic for future research. Since spatial heterogeneity affects ecology and evolution in important and complex ways (e.g., Doebeli and Dieckmann, 2003), it is currently unclear to us whether or not such heterogeneity could naturally be integrated into the EDA approach.

Connections with immigration-based community assembly

This study clarifies why evolutionary attainability does not imply evolutionary restorability. In studies of community assembly, a similar distinction between the possibility to reach a final community and the possibility to reconstruct it through immigration has frequently been highlighted (Pimm, 1991; Law and Morton, 1996; Warren and Law, 2003). In such studies, the final communities – referred to as, e.g., invasion-resistant communities (Drake, 1990) or permanent endpoints (Law and Morton, 1996) – are constructed through successive invasions from a regional species pool. Law and Morton (1996) distinguish between permanent endpoints that possess a reassembly path and those that do not. A community with a reassembly path can be reconstructed through successive immigration of the constituent species. Such a community thereby possesses an inherent restoration mechanism through immigration, just as an evolutionarily restorable community does through gradual evolution. Permanent endpoints that lack reassembly paths, on the other hand, can only be constructed through invasion sequences involving catalyst species that are lost again during the further assembly process (Law and Morton, 1996; Pimm, 1991). Such communities can be subject to a so-called Humpty-Dumpty effect (Pimm, 1991): once broken, they cannot be put together again from their pieces. Another, even more severe, consequence of extinction in communities without a reassembly path may be 'community closure.' In that case, the post-extinction community cannot be invaded by any species of the considered species pool, which implies, in particular, the impossibility of reinvasion of those species that vanished in the extinction event (Lundberg *et al.*, 2000).

We can easily extend these notions from immigration-based community assembly to evolutionary community assembly. In ESS communities that are not fully restorable, evolutionary Humpty-Dumpty effects and evolutionary community closures may occur when an ESS configuration can be attained through gradual evolution from a single species, but is not restorable by these processes after an extinction. For example, the dimorphic CSS in Figure 4 experiences an evolutionary Humpty-Dumpty effect (when the non-evolving competitor is not considered to reinvade through immigration). Similar phenomena give rise to 'evolutionary hysteresis' effects in adaptive dynamics models of seed-size evolution (Geritz *et al.*, 1999) and in the evolution of genetic polymorphism in heterogeneous environments (Kisdi and Geritz, 1999). The general prerequisite for these effects to occur, the coexistence of several alternative evolutionarily attracting community configurations, seems widespread and has, for example, been reported for evolutionary models of foraging behavior (Brown, 1990), predator-prey interactions (Dieckmann *et al.*, 1995), asymmetric competition (Law *et al.*, 1997), and cannibalism (Dercole, 2003).

Connections with the concept of keystone species

Keystone species, often defined as species that are crucial for maintaining the organization and diversity of an ecosystem (Paine, 1966; Mills *et al.*, 1993), have attracted much attention in community ecology in general, and in community-assembly studies in particular. The concept was placed into an evolutionary context by Brown and Vincent (1992), as mentioned in the Introduction. Our study suggests a natural generalization: a species is an 'evolutionary keystone' if its removal causes a community to shift from one EDA to another. This generalized definition captures the gist of Brown and Vincent's idea, since in their study the removal of a keystone predator caused a shift to a different ESSs (with fewer prey strategies). In the shared trait-space models we have studied here, evolutionary keystone species are thus defined as species with extinction projections that fall outside of the current EDA (Fig. 3B and 3C). If one preferred the concept of keystone species to be associated with a positive effect on diversity, one could restrict it to cases in which the EDA shift caused by extinction of the keystone species implies a further reduction in the total number of species.

Connections with empirical studies of diversification and adaptive radiation

Evolutionary restorability can be considered as a particularly strong stability notion, requiring evolutionary attainability from several starting points, as well as ecological coexistence not only in the final community but also along the paths of evolutionary restoration. It may be unlikely that these strict requirements hold for natural communities, especially when these are large. Yet, if a community, or a part thereof, had this property, it could be expected to appear again and again.

Indications that such evolutionary determinism is indeed possible come from observations of parallel speciation in different organisms (Schluter, 2000; Johannesson, 2001) and of repeated adaptive diversification in natural (Losos, 1994) and experimental systems (Rainey and Travisano, 1998; Friesen *et al.*, 2004). Using the terminology of this study, however, one may say that such evidence only corroborates the evolutionarily attainability of the observed community configurations, and is not necessarily telling us whether these communities are evolutionarily restorable or how their EDAs may be organized. One way to obtain deeper insights into the latter questions is to study how species removal or major perturbations alter the selection pressures on species in communities with well-studied evolutionary ecology, such as the *Anolis* lizards (Losos, 1994; Schoener *et al.*, 2001). Also studies on adaptive radiations and immigration history in spatially structured microcosms, of species such as *Pseudomonas fluorescens*, may provide relevant clues. Interestingly, adaptive radiation in these bacterial microcosms is possible if the system is initiated by an ancestral genotype (SM, which forms smooth colonies), but can be blocked if one of the derived genotypes (small-WS; known as "wrinkly spreader") is introduced into the microcosm shortly after or before the ancestral genotype (Fukami *et al.*, 2007). Likewise, Rainey (2005) found that adaptive radiation in *P. fluorescens* may lead to different community compositions depending on which of the derived strains the systems is initiated with. This sensitivity to initial conditions indicates the presence of several EDAs and suggests that evolution will take different courses after extinctions depending on which of the derived species remained in the community. If it were possible to delineate EDAs in these or other natural systems, even in a coarse way, exciting perspectives for evolutionary community ecology would result.

Connections with evolutionary restorations after mass extinctions

The relevance of insights reported here for understanding large-scale processes of evolutionary restoration, such as those occurring after mass extinctions (Jablonski, 1989; Erwin, 2001), is difficult to establish. It has often been argued that ecological interactions play a relatively small role in producing patterns found in the fossil record (Jackson, 1994; Ivany, 1996; DiMichele *et al.*, 2004). Instead, the importance of historical contingencies for evolutionary processes has frequently been emphasized (Gould, 1989). Yet it is interesting to note that features highlighted in this study can be related to some of the complex patterns found in studies of large-scale biotic recovery.

To start with, we have seen that evolutionary restoration may involve extinctions driven by evolution (Fig. 4). Such extinctions may occur a long time after the initial extinction and can be seen as a small-scale analogue of a "dead clade walking" – a pattern observed in fossil records, describing lineages that survive mass extinctions only to go extinct in the subsequent recovery process (Jablonski, 2002).

Studies of the fossil record also indicate delays of several million years in the onset of biotic recovery after mass extinctions, during which little diversification takes place (Sepkoski, 1998; Kirchner and Weil, 2000; Erwin, 2001). The EDA approach draws attention to several phenomena that may contribute to such lags in evolutionary restoration processes. First, one may expect delays in the buildup of high diversity when communities get stuck at low-diversity ESSs from which they cannot easily escape due to evolutionary community closure. Second, the emergence of communities with evolutionary Humpty-Dumpty effects, likely to be broken by extinctions, does not result in long-lasting increases in diversity. Finally, bottlenecks in the restoration process may result from speciation obstacles, which make it harder for ESS communities to be attained.

Several major extinction events in the fossil record are associated with drastic changes of the course of evolution and the appearance of new organism groups with unprecedented forms and functions (Jablonski, 1989; Sepkoski, 1998; Archibald and Deutschmann, 2001). In complex systems, one must expect that extinctions, by causing a community to shift from one EDA to another, will occasionally open avenues to multispecies ESSs with enhanced diversity that may otherwise be inaccessible from initial community compositions. If further studies were to show that extinctions can in this way initiate the radiation of novel taxa, they would give game-theoretical support to the view of extinctions as crucial determinants of evolutionary breakthroughs (Vermeij, 1987; Raup, 1994; Feduccia, 1995).

Biotic recovery after mass extinctions has been described as a process of refilling vacant niches and reoccupying adaptive peaks (Harries and Kauffman, 1990; Eldredge, 1997). This deterministic view of evolution has been opposed by authors who emphasize the role of developmental and genetic constraints, through the conservation of inherited body plans and historical contingencies in the genotypic representation of phenotypes, for explaining why post-extinction evolutionary trajectories do not simply restore pre-extinction communities (Conway Morris, 1998; Jablonski, 2001). Here we have demonstrated that frequency-dependent selection resulting from eco-evolutionary feedback may bring about ESSs that are not evolutionarily restorable, which highlights that evolution back to pre-extinction community configurations may be highly constrained for other, ecological reasons. Our study has shown that such ecological constraints on evolutionary restoration processes can already be observed in very simple models.

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APPENDIX A: ATTACK-RATE FUNCTION

We constructed an attack rate function $\alpha(z)$ using the function $\tilde{\alpha}(\tilde{z}) = \tilde{z}^s$ as a starting point. This latter function has been employed for constructing nonlinear trade-offs in several earlier studies (Meszéna and Czibula, 1997; Kisdi and Geritz, 1999; HilleRisLambers and Dieckmann, 2003; Egas *et al.*, 2004; Parvinen and Egas, 2004).

For a trade-off to exist, an increase in the attack rate on one prey must always be associated with a decrease of the attack rate on the other. The previously used function, however, is not directly suitable for our purposes, owing to two unrealistic, or at least extreme, features pertaining to pure specialists ($z = 0$ or $z = 1$). First, when $s < 1$, there is a marginal cost, but an infinite marginal benefit, for specialist consumers to slightly increase their attack rate on the alternative resource, since $\tilde{\alpha}'(0) = \infty$. Second, for $s > 1$, a pure specialist that slightly increases its attack rate on the alternative resource will experience a marginal cost, but no marginal benefit, since $\tilde{\alpha}'(0) = 0$. As a result of these two observations, the selection gradients for pure specialists would always be either infinite (for $s < 1$) or zero (for $s > 1$).

We therefore adjust the attack-rate function so that selection gradients for pure specialists remain finite. As shown in Figure A1, we achieve this by restricting the interval $[0,1]$ for $\tilde{z}$ to $[D,1-D]$, with $0 < D < 1/2$. We then linearly rescale $\tilde{z} \in [D,1-D]$ to $z \in [0,1]$ and $\tilde{\alpha} \in [D^s,(1-D)^s]$ to $\alpha \in [0,1]$, to obtain our function $\alpha(z)$. The parameter D affects the trade-off close to the boundaries $z = 0$ and $z = 1$ by ensuring a slope $\alpha'(0)$ that is never infinite or zero. In our examples, we use a small value for D, $D = 0.02$, which means that its effect is mostly restricted to the vicinity of the limiting trait values $z = 0$ and $z = 1$. For alternative formulations of trade-offs with finite marginal benefits for pure specialists, see Diekmann et al. (2005).

APPENDIX B: EDA CALCULATIONS FOR MODEL FOOD WEBS

We start by describing assumptions and notation common to the specific two food-web models analyzed in this study (Fig. 3 and 4). The population density of an evolving consumer i is denoted by N_i, and the population density of a resource j is denoted by R_j. The attack rates of consumer i on prey j is denoted by α_{ij}. The parameter λ is a dimensionless factor for converting consumed prey into consumers, and d is the density-independent mortality rate of consumers. In the absence of predation, resource species follow logistic growth. Time and population densities are rescaled so that the intrinsic growth rates and carrying capacities of the resources equal 1. Functional responses are assumed to be linear. As described in the main text, $z_i = 1$ means full specialization on prey 1 (i.e., resource species 1 in the first example, or the non-evolving consumer in the second example), while $z_i = 0$ means full specialization on resource species 2. We therefore set $\alpha_{11} = \alpha(z_1)$, $\alpha_{12} = \alpha(1-z_1)$, $\alpha_{21} = \alpha(z_2)$, and $\alpha_{22} = \alpha(1-z_2)$. According to the canonical equation of adaptive dynamics (Dieckmann and Law, 1996), we have $C_{ii}(\mathbf{z}) = \frac{1}{2}\mu_i\sigma_i^2 N_i^*(\mathbf{z})$, where μ_i denotes the mutation probability and σ_i^2 the mutation variance of consumer i. The off-diagonal elements of the matrix $\mathbf{C}$ are 0. For simplicity, we set $\frac{1}{2}\mu_i\sigma_i^2 = k$. For each case studied in the examples, we derive the fitness $w(z',\mathbf{z})$ of an individual with trait value z' in the environment set by the resident consumers with trait values $\mathbf{z}$ and equilibrium population densities $N_i^*(\mathbf{z})$.

The two sections below describe how evolutionary domains of attraction (EDAs) are determined in the two examples. We follow the same procedure for both examples. We start with listing the equations governing the population dynamics. We then calculate the equilibrium population densities (results not explicitly shown below for brevity) and use these to derive the fitness of strategies in monomorphic and dimorphic resident communities. Finally, we explain how coexistence domains and EDAs are obtained. The following parameter values are used throughout this study: $\lambda = 0.1$, $d = 0.01$, and $k = 0.1$.

Example 1. Evolving consumers feeding on two resources

The population dynamics for the first example (with results presented in Fig. 3) are described by

$$\frac{dR_j}{dt} = R_j(1 - R_j - \sum_i \alpha_{ij} N_i), \tag{B1a}$$

$$\frac{dN_i}{dt} = N_i(\lambda \sum_j \alpha_{ij} R_j - d), \tag{B1b}$$

for $j = 1,2$ and $i = 1$ (one consumer species) or $i = 1,2$ (two consumer species).

By setting the left-hand side of equations B1 to zero, we obtain equilibrium population densities as functions of the resident trait values; these are denoted, e.g., by $R_1^*(z_1)$, with the asterisk indicating equilibrium values. The invasion fitness (Metz *et al.*, 1992) of an individual with trait value z' in the environment set by a single resident consumer with trait value z_1 is given by that individual's per capita growth rate,

$$w(z', z_1) = \lambda\alpha(z')R_1^*(z_1) + \lambda\alpha(1 - z')R_2^*(z_1) - d\,. \tag{B2a}$$

With two resident consumers, invasion fitness becomes

$$w(z', \mathbf{z}) = \lambda\alpha(z')R_1^*(\mathbf{z}) + \lambda\alpha(1 - z')R_2^*(\mathbf{z}) - d\,. \tag{B2b}$$

The sections of the monomorphic diagonal along which a single consumer is viable are established by $N_1^*(z_1) > 0$. The coexistence domains for two consumer species are established by mutual invasibility (Metz *et al.*, 1996) using equation B2a, $w(z_1, z_2) > 0$ and $w(z_2, z_1) > 0$. For the parameter values in Figures 3E and 3F, the trait value $z_1 = 1/2$ is a branching point, $\partial^2 w(z', z_1)/\partial z'^2\big|_{z'=z_1} > 0$. In Figures 3C and 3D, by contrast, species with $z_1 = 1/2$ are not viable.

For Figure 3F, dimorphic evolutionary dynamics are deduced using the geometric method presented by Rueffler *et al.* (2004) and utilized in Diekmann *et al.* (2005) in an application similar to the one studied here. Given the linear invasion boundary and the concave trade-off curve, continuous adaptation in the dimorphic community will lead to $(z_1, z_2) = (1,0)$ from any point in the coexistence domain. In the cases shown in Figures 3D and 3E, there may be a monomorphic repellor between the diverging traits in the dimorphism. In such cases, mutual invasibility cannot be guaranteed, as explained in Rueffler *et al.* (2004), and therefore the geometric method may not apply. In these cases, EDAs were established numerically, by calculating evolutionary trajectories using equation B4 in conjunction with the corresponding canonical equations. Initial trait values were uniformly distributed in the two-dimensional trait space, with distances 10^{-3} in the directions of z_1 and z_2. By recording where the trajectories of gradual evolution ended up, the EDAs were delineated.

Example 2. Evolving predators feeding on two trophic levels

The community examined in the second example (with results presented in Fig. 4) contains a non-evolving consumer in addition to two resources and the evolving predator(s). We denote the population density of the non-evolving consumer by M and assume that it feeds on resource species 1 with an attack rate of 1. The resultant population dynamics are described by

$$\frac{dR_1}{dt} = R_1(1 - R_1 - M)\,, \tag{B3a}$$

$$\frac{dR_2}{dt} = R_2(1 - R_2 - \sum\nolimits_i \alpha_{i2} N_i)\,, \tag{B3b}$$

$$\frac{dM}{dt} = M(\lambda R_1 - \sum\nolimits_i \alpha_{i1} N_i - d)\,, \tag{B3c}$$

$$\frac{dN_i}{dt} = N_i(\lambda \alpha_{i1} M + \lambda \alpha_{i2} R_2 - d)\,, \tag{B3d}$$

for $i = 1$ (one predator species) or $i = 1,2$ (two predator species).

The invasion fitness of an individual with trait value z' in the environment set by the resident predator(s) is calculated as in the first example, which gives

$$w(z', z_1) = \lambda \alpha(z') M^*(z_1) + \lambda \alpha(1 - z') R_2^*(z_1) - d \tag{B4a}$$

for one resident predator and

$$w(z', \mathbf{z}) = \lambda \alpha(z') M^*(\mathbf{z}) + \lambda \alpha(1 - z') R_2^*(\mathbf{z}) - d \tag{B4b}$$

for two resident predators.

We find that a single predator is viable, $N_1^*(z_1) > 0$, along the entire monomorphic diagonal. We establish the coexistence domain of the three consumer species by checking where in the two-dimensional trait space all three species have positive equilibrium densities. These ecological equilibria are locally stable, which is confirmed by checking that the eigenvalues of the Jacobian of the population dynamics have negative real parts. It can also be shown that, for any point in the coexistence domain, successive immigrations can establish the full community (Law and Morton, 1996).

For the parameter values in Figure 4, monomorphic evolution leads to a branching point at which the predator may split up in two species. For analyzing the subsequent dimorphic evolution, we again utilize the geometric method by Rueffler *et al.* (2004). Since the invasion boundary is linear (eq. B4b) and the trade-off curve is concave for the parameters in Figure 4, we conclude that trait values will diverge through continuous adaptation and finally reach $(z_1, z_2) = (1,0)$. This means that one of the two predator species becomes a top predator in a linear food chain, while the other predator species specializes on the other resource.

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FIGURE CAPTIONS

Fig. 1. Evolutionary domain of attraction (EDA) of a dimorphic ESS. In A, monomorphic evolutionary dynamics occur along the diagonal ($z_1 = z_2$), while dimorphic evolutionary dynamics occur outside the diagonal ($z_1 \neq z_2$). The evolutionary domain of attraction includes the central, dark-gray interval of the diagonal, but not the surrounding light-gray intervals. The ESS can be attained from all monomorphic and dimorphic trait-value combinations within the EDA. The EDA and coexistence domain are symmetric around the diagonal, but only the lower parts are shown here to avoid redundancy. In B, adaptive landscapes (invasion fitness w as a function of trait value z) are shown for three different trait-value combinations (points a to c) in A.

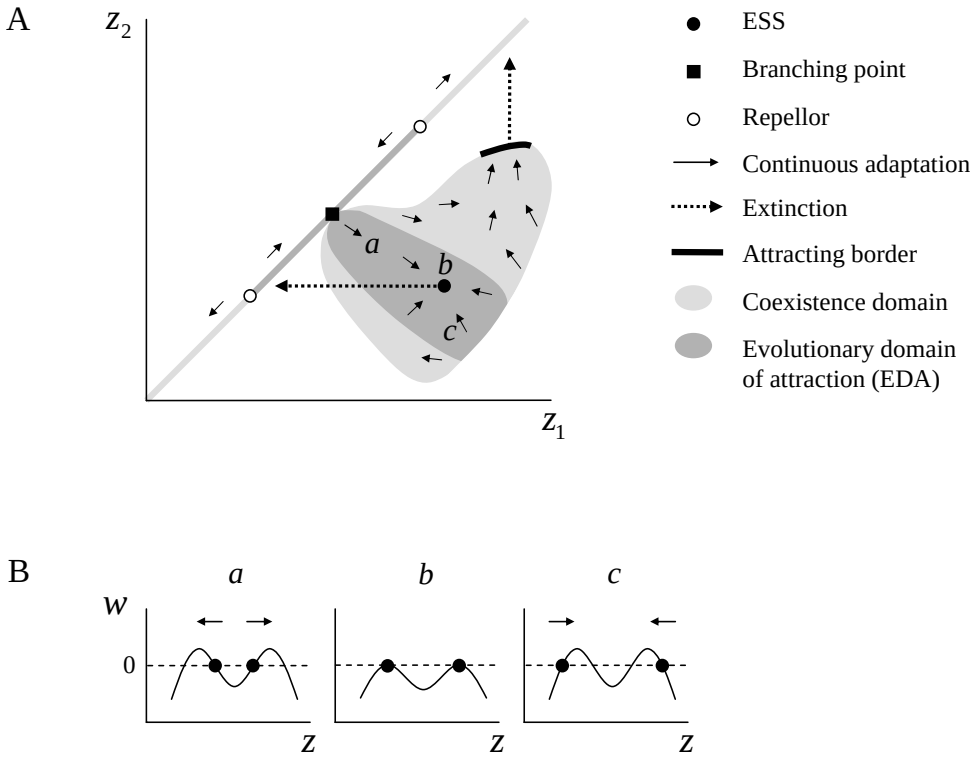
Fig. 2. Full classification of the evolutionary attainability and restorability of dimorphic ESSs. Coexistence domains are not shown.

Fig. 3. Evolutionary domains of attraction (EDAs) for evolving consumers feeding on two resources under different trade-offs. In A, the attack rate $\alpha(z)$ on resource species 1 and the attack rate $\alpha(1-z)$ on resource species 2 are plotted against each other for different trade off strengths s. Different food-web configurations (B) and their corresponding trait-value combinations (C to F) are labeled a, b, and c. In B, the two resource species (open circles) are connected to consumers (filled circles) by continuous lines if the corresponding attack rates equal 1, implying full specialization. Otherwise, these connections are shown as dashed lines. In C to F, dark-gray regions represent the EDA of the dimorphic CSS c, and light-gray regions represent the EDAs of the monomorphic CSSs a and b. Dashed sections of the monomorphic diagonals indicate trait values for which a single species is not viable. Dashed curved lines in E separate regions where dimorphic trajectories lead to the dimorphic CSS directly from regions where the dimorphic CSS is reached via extinction. Parameters: $s = 4$ (D), $s = 2$ (E), and $s = 1.5$ (F).

Fig. 4. Evolutionary domains of attraction (EDAs) for evolving predators feeding on two trophic levels under different trade-offs. Different food-web configurations (A) and their corresponding trait-value combinations (B) are labeled a to f. In A, the non-evolving consumer is represented by a gray circle, otherwise food-web configurations are shown as in Figure 3. The arrows in A represent transitions between different food-web configurations through gradual evolution (solid arrows), extinction (dotted arrows) or invasion (dotted and shaded arrow). In B, dark-gray regions represent the EDA of the dimorphic CSS c, and light-gray regions represent the EDA of the monomorphic CSS f, consisting of a single specialist. Filled triangles indicate trait values at which the non-evolving consumer goes extinct (transition e-e'). The lower instance of the monomorphic diagonal (with the black z_2-axis on the left) corresponds to a community containing the non-evolving consumer, while the vertically displaced upper instance of the monomorphic diagonal (with the gray z_2-axis on the right) corresponds to a community lacking the non-evolving consumer. The interval of the monomorphic diagonal marked with a black outline close to f is the range across which the non-evolving consumer can reinvade the community. Dashed sections of the monomorphic diagonals indicate trait values for which a single species is not viable. Parameter: $s = 1.3$.

Fig. 5. Example of a fully evolutionarily restorable trimorphic CSS. The CSS consists of species numbered 1, 2, and 3. In A, an example of community evolution in shown, punctuated by three environmentally driven extinctions. The initial monomorphic trait value is represented by a filled star. The monomorphic trajectory is represented by a dashed line, while di- and trimorphic trajectories are represented by thin and thick continuous lines, respectively. Extinctions are marked with horizontal dotted lines numbered according to which of the species in the CSS goes extinct. Trait values of the dimorphic branching point are marked with gray vertical lines and filled squares, while trait values of the trimorphic CSS are marked with black vertical lines and filled circles. In B, the mono- and dimorphic parts of the CSS's EDA are shown (whereas, for the sake of greater visual clarity, the trimorphic parts of this EDA are not shown). The entire monomorphic diagonal is included in this EDA. Evolutionary trajectories corresponding to the time series in A are shown in B. Extinction projections in B are represented by numbered dotted arrows and correspond to the extinctions shown in A. There are six redundant mirror images of the trimorphic CSS and its EDA, of which only one is shown.

Fig. A1. Attack-rate function. The attack-rate function $\alpha(z)$ used in this study is shown as a thick curve, with coordinate axes given by the dashed box. The function $\tilde{\alpha}(\tilde{z}) = \tilde{z}^s$ from which $\alpha(z)$ was derived, as described in Appendix A, is shown as a thin curve, with coordinate axes given by the continuous straight lines. Parameter: $s = 2$.



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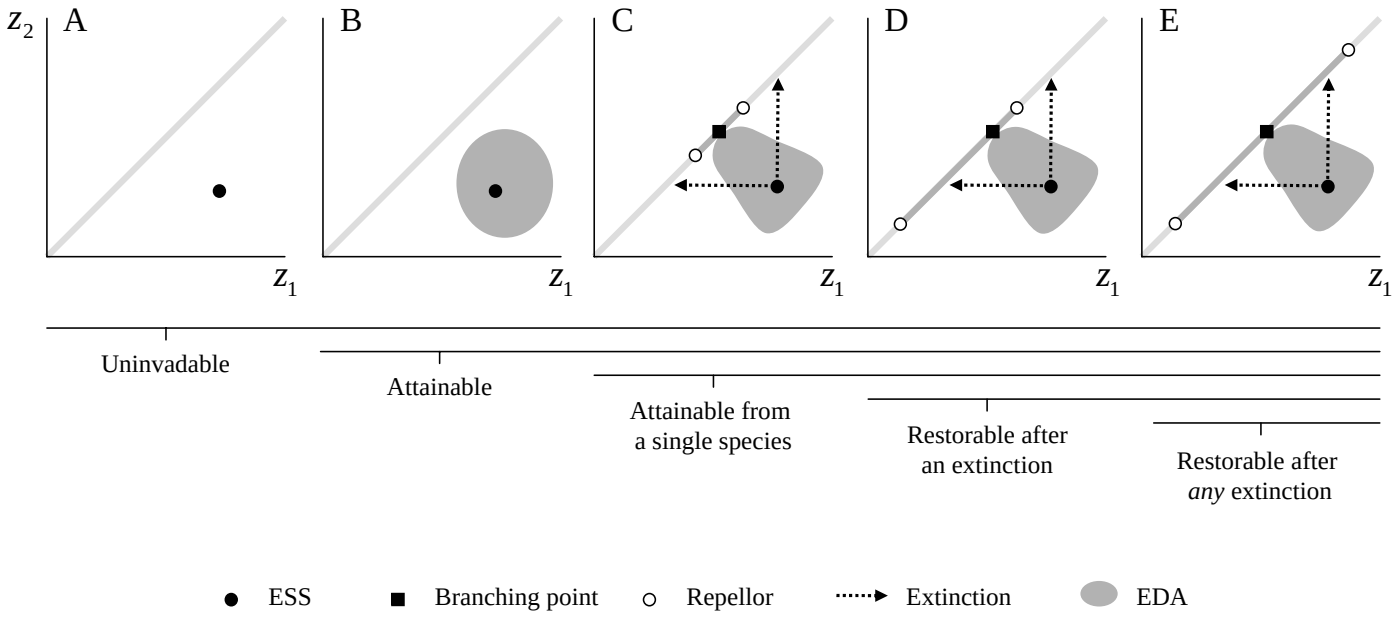

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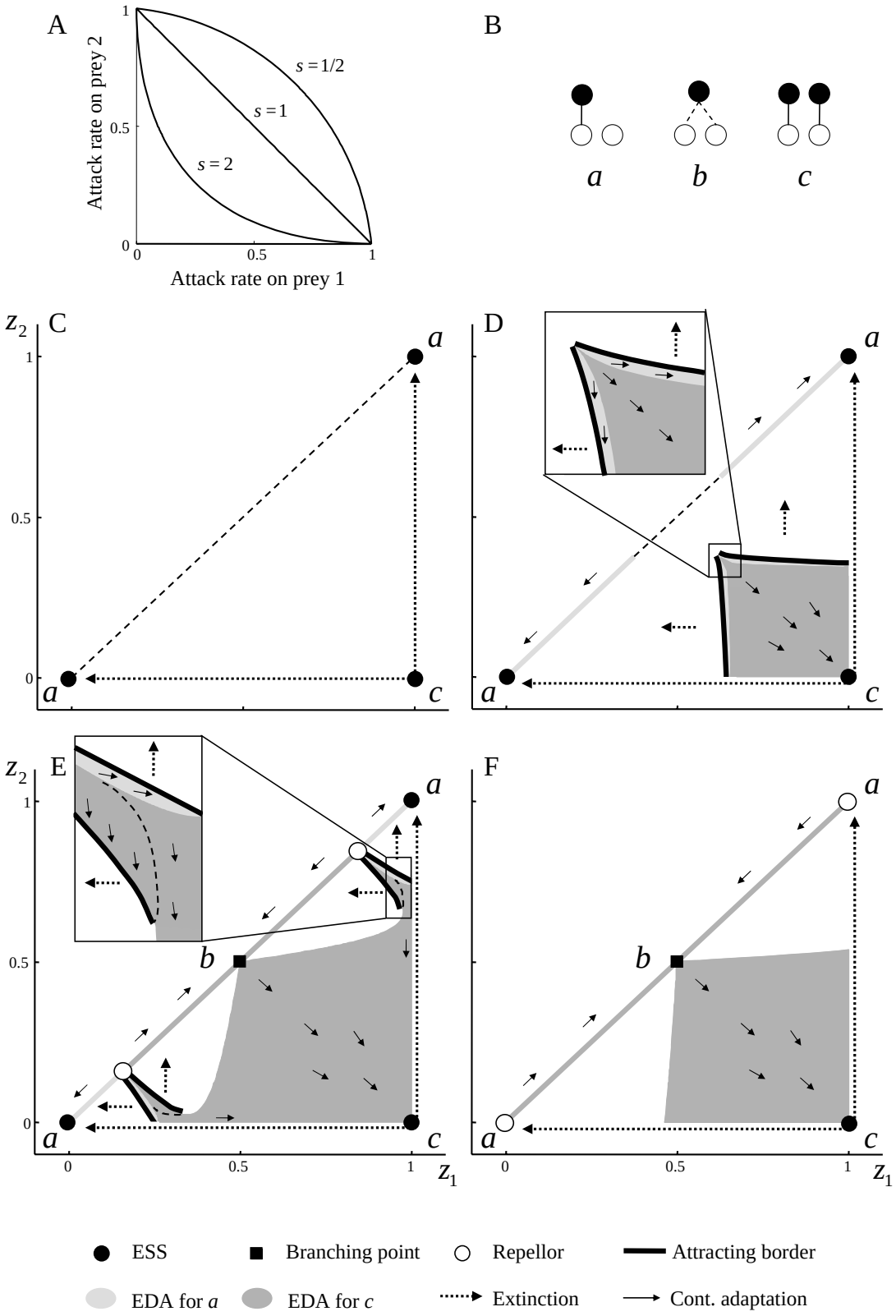
A
Attack rate on prey 2
Attack rate on prey 1
s = 1/2
s = 1
s = 2
0
0.5
1
B
a
b
c
C
D
E
F
z2
z1
ESS
Branching point
Repellor
Attracting border
EDA for a
EDA for c
Extinction
Cont. adaptation

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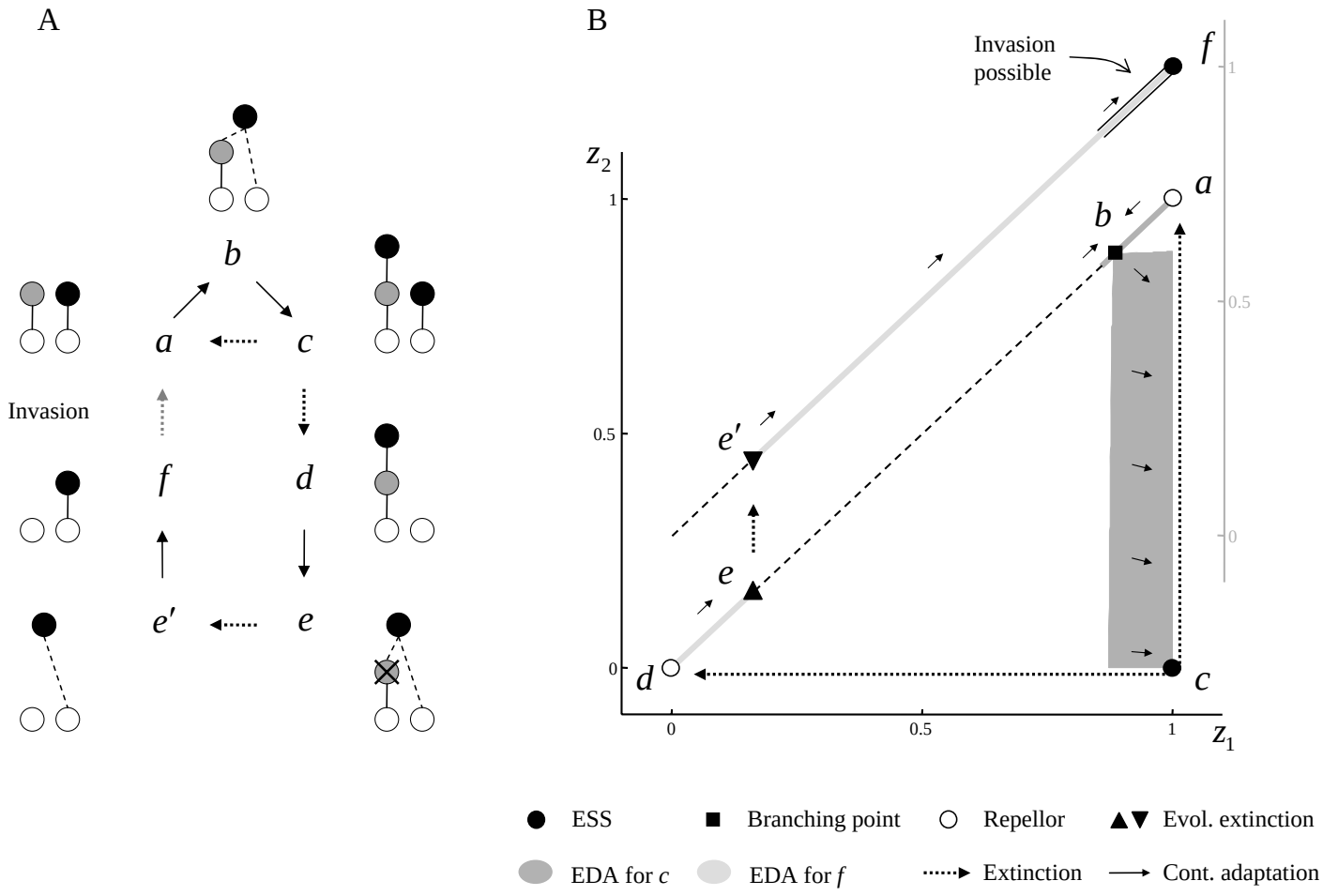

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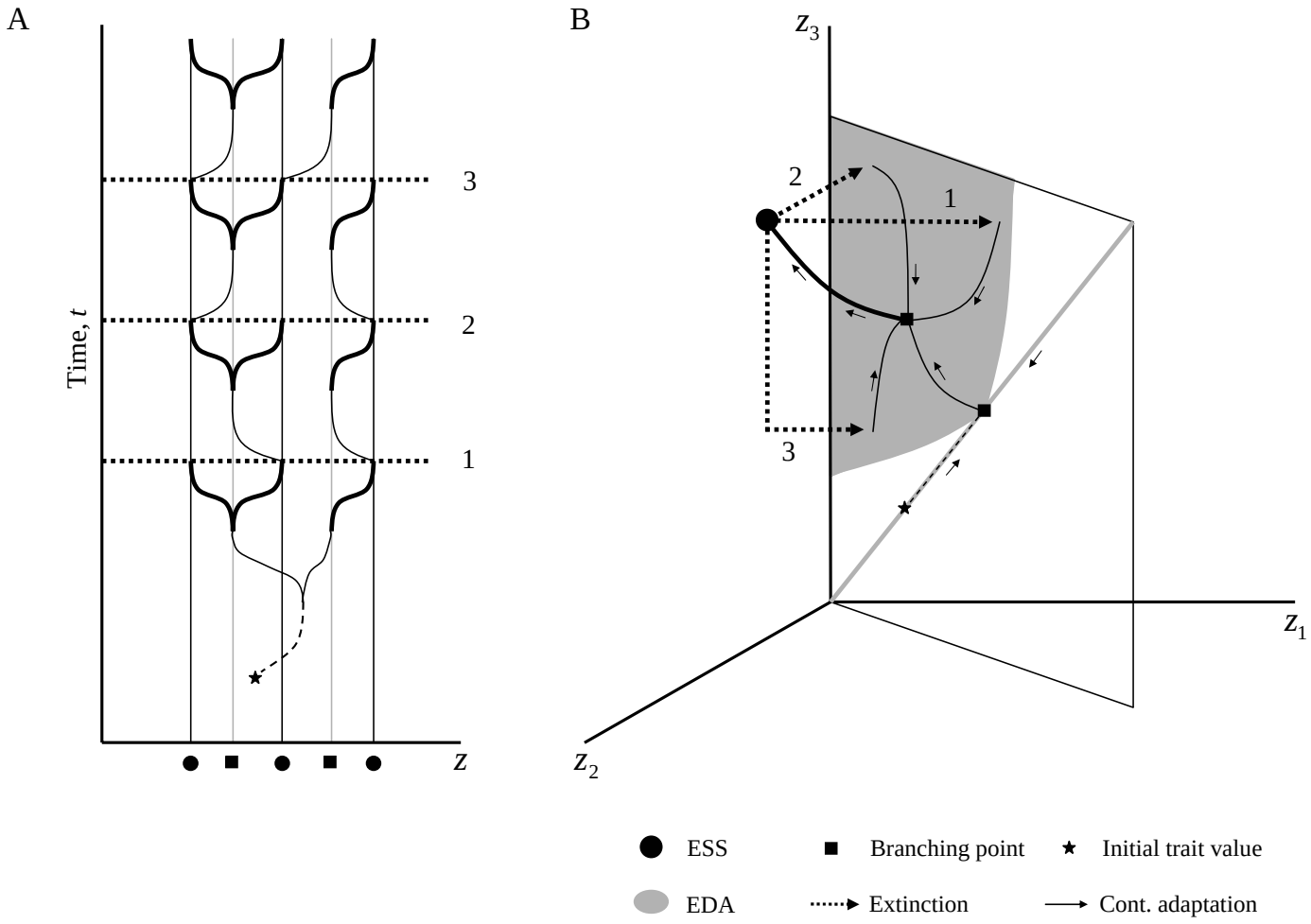

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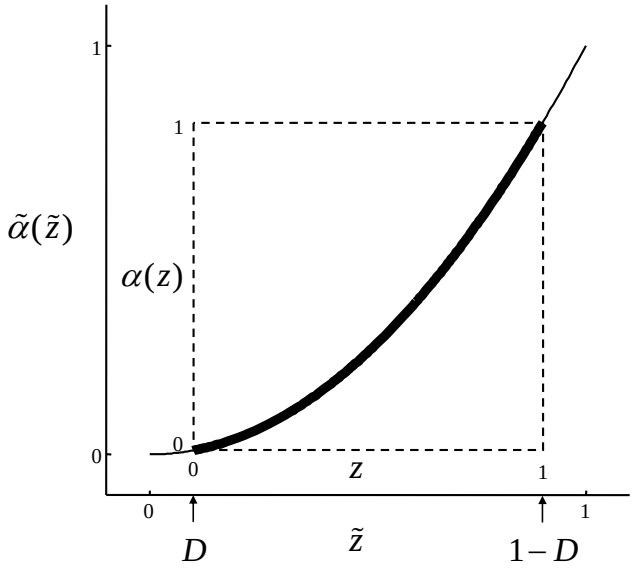

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