

Animal Ecology
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Multidimensional Adaptive Dynamics and evolutionary diversification

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1 Eco-evolutionary feedback, disruptive selection, and the origins of diversity

The mechanisms responsible for the origin and maintenance of biological diversity have been a centerpiece of evolutionary biology for almost two hundred years [6]. Growing evidence coming from both theoretical and empirical studies disputes the Modern Synthesis' view that fitness landscapes are fixed, and that ecological processes occur at too fast a pace to influence evolutionary outcomes [35, 8, 13]. Instead, a feedback exists between ecological and evolutionary processes: organisms adapt to selective pressures, which are the product of their current genetic and phenotypic makeup in relation to the whole range of ecological interactions afforded by the environment – climate, geography, predators, prey, parasites, competitors, etc. In turn, organisms modify the environment (e.g. densities of resources, competitors, parasites, etc) in ways that can affect further ecological interactions, and the organism's own evolutionary outcomes as well as that of other species [27] (Figure 1).

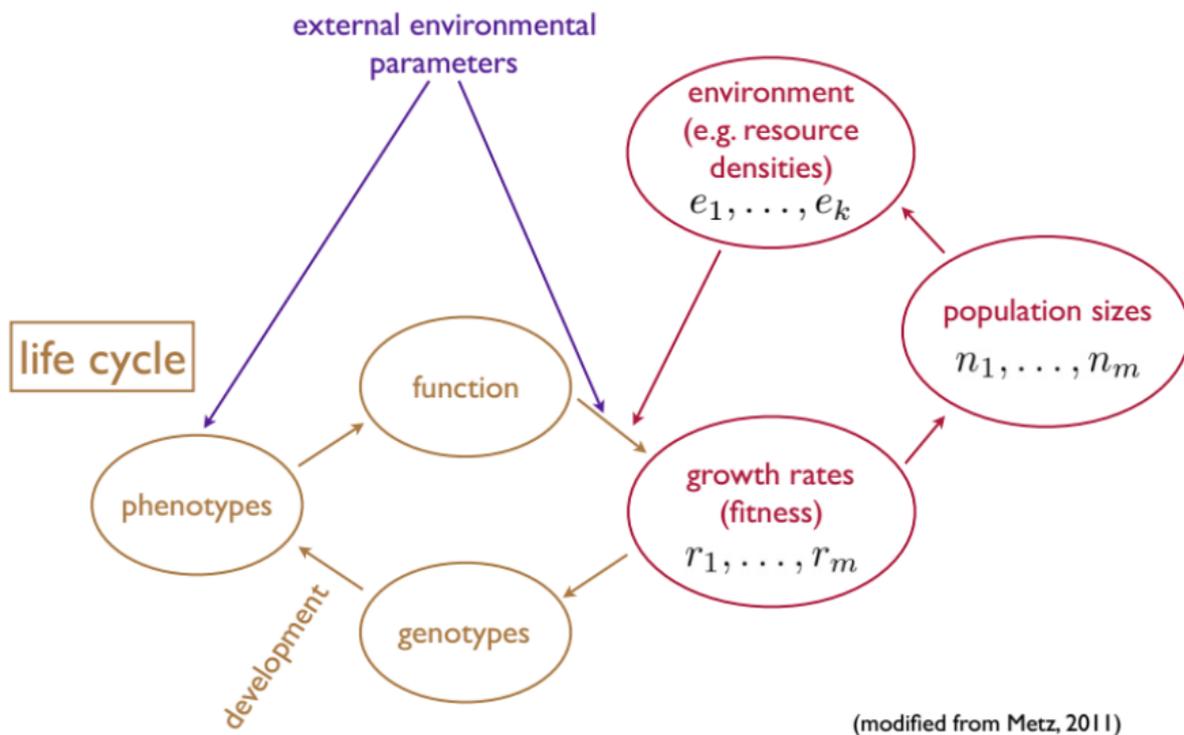


Figure 1: Eco-evolutionary feedback loop

Disruptive selection regimes – which occur when more extreme phenotypes are favored over

intermediate ones – had been recognized in the past for potentially contributing to the evolution of phenotypic diversity [26? , 40]. Later, as Rueffler et al. [33] point out, frequency-dependent disruptive selection was acknowledged as an important element driving phenotypic diversification [8, 11]. This type of selection arises due to ecological interactions such as competition, predation, parasitism, etc, and can be split into two categories: a positive frequency-dependence relation, where a phenotype has a fitness advantage if it is more frequent; and a negative frequency-dependence relation, where a phenotype has a fitness disadvantage if it is more frequent. It is negative frequency-dependent disruptive selection that is linked with potential for diversification [28, 33].

Negative frequency-dependent disruptive selection regimes may come about as follows: a population experiencing directional selection moves uphill on the fitness landscape towards an attractor of the evolutionary dynamics, for example, when it evolves to exploit the most abundantly distributed resource. Yet, due to frequency-dependent interactions between the organisms and their environment, the fitness landscape itself changes as the population evolves, such that what was once a fitness peak turns into a valley. For instance, when the phenotype best suited to feed on a type of resource becomes more abundant, it may deplete those resources, thus creating a common type disadvantage. Such attractors of the evolutionary dynamics that become fitness minima when reached are *evolutionary branching points* (Figure 2). In the vicinity of evolutionary branching points similar phenotypes can coexist in a protected polymorphism and experience further divergent selection. This can lead to a range of diversification scenarios, e.g. increased phenotypic variation due to genetic or plastic effects, sexual dimorphism, or the splitting of one lineage into two [33].

1.1 What we know from theoretical and empirical studies

Evolutionary branching occurs in many mathematical models that derive fitness from ecological scenarios that account for competition, predation, and pathogens, which lead to density and frequency-dependent selection [13]. These are only a few examples of many mathematical models where evolutionary branching occurs when ecology is explicitly taken into account (<http://www.mv.helsinki.fi/home/kisdi/addyn.htm> for a list of such models): for instance, Kisdi

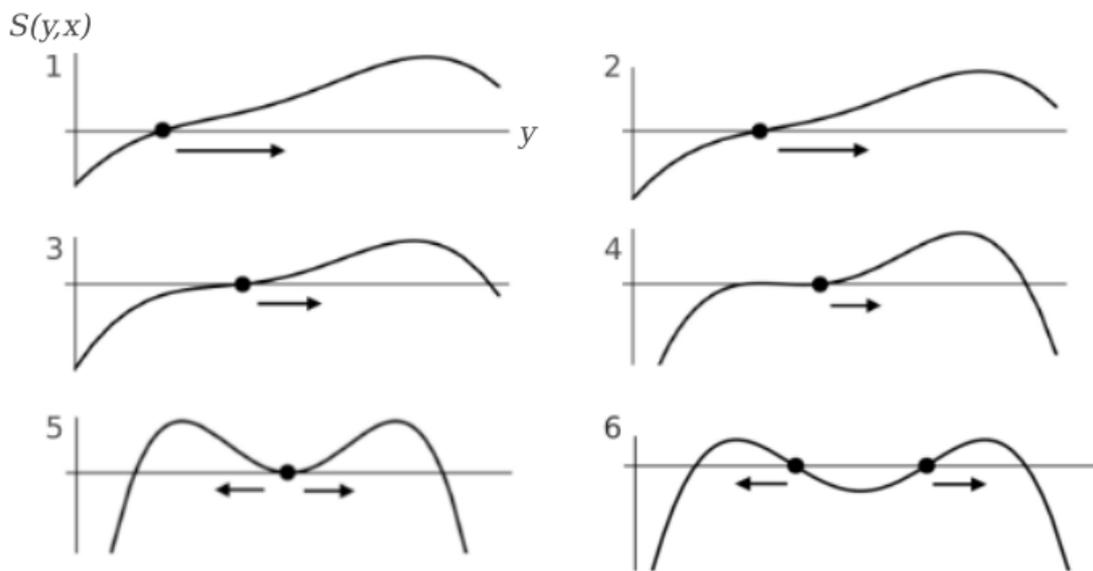


Figure 2: Shifting fitness landscapes. Mutant's invasion fitness as a function of mutant's trait value. Black dot represents resident's trait value and arrow gives the direction of trait evolution.

and Geritz [21] find evolutionary branching in a model of evolution of genetic polymorphism in a heterogeneous environment when there is frequency-dependent disruptive selection due to competition. Day et al. [7], while investigating the evolution of life-history strategies, find that branching could only occur in a food web model in which predator and prey population dynamics are ecologically coupled such that they interact in a density-dependent manner. In addition, Rueffler et al. [34] detect branching exclusively in foraging traits that mediate consumer-resource interactions in a frequency-dependent manner, so that organisms which specialize in the lesser consumed resource have an advantage.

Also, ample empirical evidence exists for phenotypic diversification due to negative frequency and density-dependent interactions driving disruptive selection regimes in natural populations [2, 35, 36], which lends explanatory power to the theory. For example, Bolnick and Lau [4] observed that disruptive selection occurs in a predictable pattern in threespine sticklebacks inhabiting postglacial lakes. They found that selection on trophic morphology is strongest in intermediate-sized lakes that have the most even distribution of resources and thus maximize frequency-dependent interactions as well as the availability of alternative resources. This way, individuals are able to specialize in either one or the other resource, and thus mitigate the effects

of intraspecific competition. On the other hand, neither small nor large lakes displayed significant signs of disruptive selection because of higher resource homogeneity in these habitats. In another example, now from the lab, Herron and Doebeli [19] documented the evolutionary dynamics of adaptive diversification in three replicate evolution experiments using *E. coli*. This bacterium preferentially metabolizes glucose and excretes acetate until that resource is depleted, and then undergo a switch to acetate consumption. The authors find that evolutionary branching is induced by a process where the appearance of one phenotype (the slow switcher from glucose to acetate metabolism) caused changes in the ecological environment, which in turn allowed the invasion of the alternate phenotype (the fast switcher). Herron and Doebeli claim that this process closely resembles the evolutionary dynamics seen in mathematical models of adaptive diversification due to frequency-dependent ecological interactions, and therefore diversification follows a predictable evolutionary pattern.

1.2 What we do not know very well

Despite the ubiquity of evolutionary branching phenomena, theoretical results published so far are mostly restricted to models based on one single quantitative trait (a growing list of such papers can be found at <http://www.mv.helsinki.fi/home/kisdi/addyn.htm>). This is insufficient when we consider that organisms in nature have many coevolving traits. The few models that do consider multidimensional trait spaces have yielded conflicting results, with some showing that increasing the number of co-evolving traits can either favor [32, 14, 39, 15, 38] or hinder diversification [1, 41, 24, 39, 15]. Consequently, we are left without comprehensive knowledge of how realistic representations of biological organisms affect the potential for evolutionary diversification, or of the specific set of circumstances that lead to different outcomes. In fact, we have to wonder whether the dichotomy facilitation vs. hindrance is the right way to think about these possible outcomes. To better understand this relationship, and how it might be instantiated in nature, it is crucial to develop models that describe with realism the effects of complex organisms interacting with their environment.

In the following sections, I will briefly go through the mathematical modeling framework of *adaptive dynamics*, which has been very successful in investigating the phenomenon of biological

diversification. I will start by laying out core concepts in one-dimensional analysis. Then, I will move on to the mathematics behind the same concepts in many dimensions, and review some of the studies that have shown either a positive, a negative, or a mixed effect of multidimensionality on evolutionary branching. Finally, I will give an overview of the current state, and point to progress that can be made in the future.

2 Adaptive dynamics framework in one dimension

2.1 Motivation

Adaptive dynamics – also known as evolutionary invasion analysis – is a mathematical framework developed in the 1990’s to study long term evolution of quantitative traits as driven by mutation and substitution events. It is based on evolutionary game theory and dynamical systems theory, and combines these into a powerful modeling framework. One of the defining features of adaptive dynamics is that it derives the fitness function of phenotypes from explicit ecological scenarios, taking into account frequency and density dependent interactions, spatial and temporal structure, etc. It allows one to analyze complex evolutionary questions from an ecologically realistic perspective [16, 43, 22, 5].

The main goal of an adaptive dynamics analysis is understanding long-term evolution – driven by mutation and selection – by assessing the growth rate of an initially rare mutant in a resident community. Will the mutant be able to grow and replace the resident, will it grow but not completely replace the resident, or will it go extinct? The answer to these questions tells us about the direction of trait evolution and the possibility of coexistence of different types within a population – that is, about the conditions for diversification. I will explain how this works in more detail below.

Adaptive dynamics assumes a very large population of replicators (organisms, alleles) that have clonal reproduction and are characterized by continuously varying phenotypic traits which undergo rare mutational events. The mutation steps may be of any size, but for technical reasons are often restricted to small steps because it lets one perform a linear approximation of

the mutant's fitness around the resident's trait value. The rareness of mutations allows one to separate evolutionary and ecological time scales, such that the resident population reaches its demographic attractor before a new mutant appears. Then one needs only to consider the growth rate of the mutant while it is still rare to determine if it will be able to invade and replace the resident [5]. This modeling framework is very general and can be applied to any number of traits [16, 25]. However, for reasons of mathematical tractability, it is more frequently performed on a single evolving trait.

2.2 Main concepts

In adaptive dynamics, unlike population genetics, the concept and measure of fitness is a phenotype's invasion potential [29], i.e. the mutant's ability to invade a resident community characterized by different trait values. The community can be composed of any number of types, but for simplicity is usually restricted to one type. *Invasion fitness* is defined as the long-term exponential growth of an initially rare mutant y in an environment set by the demographic attractor of the resident x [29, 16], and denoted by $S(y, x)$. An example of a demographic attractor is the asymptotically stable equilibrium of many population dynamics models, e.g. in the logistic growth model, the carrying capacity is a demographic attractor. Once reached, slight perturbations of the population tend to lead it back to the attractor. Attractors can be points, as the carrying capacity in the logistic growth model, or more complex objects like limit cycles. The predator-prey model, for instance, has both a point and a limit cycle attractor. When a resident population is at its demographic attractor, the invasion fitness of an individual with the resident trait value is zero, $S(x, x) = 0$, that is, its growth rate equals zero. So when a new mutant appears, if $S(y, x) > 0$, then it has a positive probability of spreading (it might not do so, due to demographic stochasticity), and if $S(y, x) < 0$, it will definitely go extinct (in a large enough population, which is assumed by adaptive dynamics).

Invasion fitness can be visualized as the fitness landscape experienced by rare mutants, where the landscape itself changes with each successful invasion (Figure 2). The precise expression of the invasion fitness function will depend on details of each specific model. Initially, while rare, the mutant has no impact on neither the resident population's per capita growth rate nor the

relevant environmental backdrop against which evolution plays out – predator, resource and pathogen densities are all determined by the resident population with trait value x .

For mutants that are sufficiently similar to the resident, invasion fitness can be linearly approximated by

$$S(y, x) \approx S(x, x) + \left. \frac{\partial S(y, x)}{\partial y} \right|_{y=x} (y - x). \quad (1)$$

This derivative represents the slope of the fitness landscape at the resident trait value, and is denoted by $D(x)$. If $D(x) > 0$, that means mutants with $y > x$ will be able to invade, and if $D(x) < 0$, then invasion occurs only for mutants with $y < x$.

Adaptive dynamics models evolution as an iterative process of consecutive invasions. This process stops, at least momentarily, if it reaches a point x^* where the fitness landscape is flat, $D(x) = 0$. Such points are called *evolutionarily singular points*, and are of special interest because directional selection vanishes at them. They can be either *attractors* or *repellers* of the evolutionary dynamics, and *invadable* or *uninvadable* by mutants. The four aforementioned properties can occur in any combination, and give rise to qualitatively different singular points [16, 43, 5]. I will give more detail about them below.

The evolutionary dynamics in a one dimensional trait space can be analyzed graphically by means of a Pairwise Invasibility Plot (PIP), which is a graph of the sign of $S(y, x)$ as a function of both x and y (Figure 3). PIPs allow us to see the outcomes of a series of consecutive invasions. To do so, we look along a vertical line through a point on the x-axis representing a resident strategy. Parts of this line that fall within a region marked '+' correspond to strategies on the y-axis for which $S(y, x) > 0$, that is, to mutant strategies that are able to invade the population; and the parts that fall within a region marked '-' correspond to strategies on the y-axis for which $S(y, x) < 0$, that is, to mutant strategies that cannot invade and will go extinct (Figure 3). In the next few paragraphs I will illustrate, using PIPs, four main configurations of singular points obtained from combinations of the four properties above.

A singular point x^* is uninvadable when

$$\left. \frac{\partial^2 S(y, x)}{\partial y^2} \right|_{y=x=x^*} < 0, \quad (2)$$

as per the second derivative test from calculus. This means it is a local maximum of the invasion fitness $S(y, x)$ with respect to y , and that no nearby mutants can invade once it is established. In the PIP, an imagined vertical line through x^* lies completely inside a region marked ‘-’ (Figure 3a and 3b). If the inequality is reversed, then x^* is a local fitness minimum with respect to y and any nearby mutant can invade – an imagined vertical line then lies completely inside a region marked ‘+’ (Figure 3c and 3d).

A singular point x^* is *convergence stable* – that is, an attractor of the evolutionary trajectory – if $S(y, x) > 0$ for mutants y with a trait value closer to x^* than the resident x [16]. Mathematically, this is the case when

$$\frac{d}{dx} \left(\left. \frac{\partial S(y, x)}{\partial y} \right|_{y=x} \right)_{x=x^*} < 0. \quad (3)$$

This means that around x^* the selection gradient $D(x)$ goes from positive to negative (it is positive for $x < x^*$ and negative for $x > x^*$), that is, $D(x)$ is a decreasing function of x at x^* . In the PIP there is a ‘+’ above the main diagonal to the left and below the main diagonal to the right of x (Figure 3a and 3c). If the above inequality is reversed, then x^* is a repeller of evolutionary dynamics and successive mutations will necessarily move the trait value of the population away from the point. In the PIP, you see a ‘-’ above the main diagonal to the left and below the main diagonal to the right of x (Figure 3b and 3d).

A singular point x^* that is uninvadable and convergence stable is an endpoint of evolution, given that it is a local attractor of the evolutionary dynamics and a local fitness maximum. These are called *continuously stable strategies*. A singular point that is invadable and convergence stable is of particular interest because it is an *evolutionary branching point* (Figure 3c). Monomorphic populations sufficiently close to evolutionary branching points will necessarily become dimorphic and undergo disruptive selection, leading to two diverging subpopulations [16, 43, 5]. One of the most interesting potential applications of this framework is modeling the

We can use PIPs to get the region of coexistence for protected dimorphisms. In order to do so, the original PIP (Figure 4a) is first mirrored along its main diagonal (Figure 4b), and the resulting image is then overlaid on top of the original (Figure 4c). The overlap of regions with a '+' sign in both the original PIP and its mirrored image is the region of coexistence (dark gray area in Figure 4c).

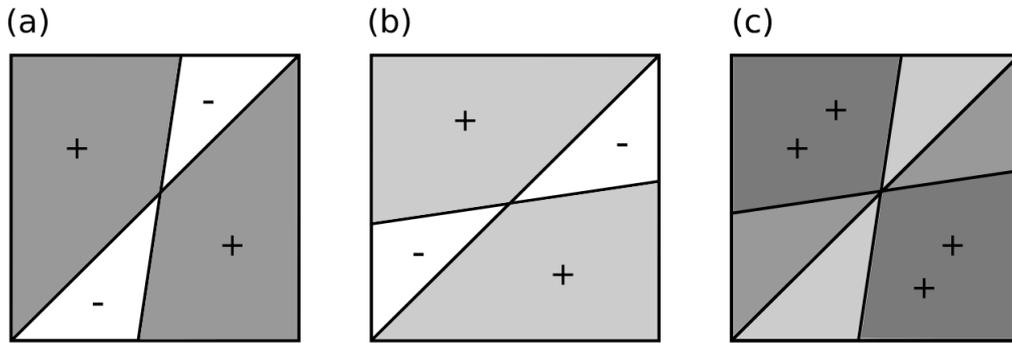


Figure 4: How to find the region of coexistence: (a) is the original PIP, (b) is its mirrored image along the main diagonal, and (c) is the image that results from overlaying (a) and (b). The region of coexistence is the dark gray area where regions marked '+' in both (a) and (b) overlap.

3 Multidimensional adaptive dynamics

It is only natural to wonder how the framework can be applied to cases of a population characterized by many coevolving traits, or to a community composed of many species, considering that biological organisms have complex phenotypes characterized by many quantitative traits. In the next few paragraphs, I will walk through the same concepts and their conditions as above, but for an analysis of multidimensional trait spaces.

A mutant's invasion fitness in a population at its demographic attractor is represented by $S(\mathbf{y}, \mathbf{x})$, where \mathbf{x} is a vector of resident phenotype trait values and \mathbf{y} is a vector of mutant phenotype trait values. Assuming – like in one-dimension – that mutations are small, the invasion fitness of the mutant is approximated by

$$S(\mathbf{y}, \mathbf{x}) \approx S(\mathbf{x}, \mathbf{x}) + \sum_{i=1}^n \left. \frac{\partial S(\mathbf{y}, \mathbf{x})}{\partial y_i} \right|_{\mathbf{y}=\mathbf{x}} (\mathbf{y} - \mathbf{x}), \quad (4)$$

where n is the dimension of the trait space. Leimar [25] characterized the conditions for invadability and convergence stability in multidimensional adaptive dynamics. What follows can be found, at greater depth, in the aforementioned article. The selection gradient in the multidimensional case is a vector whose i^{th} component is

$$\mathbf{D}_i(\mathbf{x}) = \left. \frac{\partial S(\mathbf{y}, \mathbf{x})}{\partial y_i} \right|_{\mathbf{y}=\mathbf{x}}, \quad (5)$$

where y_i is the i^{th} entry of \mathbf{y} . It gives us the slope of the fitness landscape around a resident's phenotype in the direction of trait i [25]. The canonical equation of adaptive dynamics approximates the evolutionary trajectory in the limit of infinitely small mutational increments in large populations. It is given by

$$\frac{d\mathbf{x}}{dt} = m(\mathbf{x})\mathbf{A}(\mathbf{x})\mathbf{D}(\mathbf{x}), \quad (6)$$

where $m(\mathbf{x})$ is a real-valued function describing variation in the rate of occurrence of mutations (e.g. due to variation in population size) and $\mathbf{A}(\mathbf{x})$ is the mutational variance-covariance matrix describing a symmetric distribution of mutations around the resident type \mathbf{x} [9]. Note that the canonical equation is formally similar to Lande's equation of quantitative genetics [23] which

describes the dynamics of the mean of a multivariate Gaussian trait distribution.

What holds for the one dimensional case also holds for the multidimensional case: if $S(\mathbf{y}, \mathbf{x}) > 0$, the mutant can invade the resident population; if the inequality is reversed, then the mutant will go extinct. A singular point is a point \mathbf{x}^* in trait space where the selection gradient vanishes in all directions, $\mathbf{D}(\mathbf{x}) = 0$ [25].

A singular point is uninvadable if it is a local fitness maximum. In more than one dimension, this is equivalent to the criteria that the selection Hessian, \mathbf{H} , must have all negative eigenvalues. The selection Hessian is a symmetric square matrix whose entries are given by the second-order partial derivatives of the invasion fitness function with respect to the mutant trait values and evaluated at the singular point:

$$h_{ij} = \left. \frac{\partial^2 S(\mathbf{y}, \mathbf{x})}{\partial y_i \partial y_j} \right|_{\mathbf{y}=\mathbf{x}=\mathbf{x}^*}. \quad (7)$$

If any one eigenvalue of \mathbf{H} is positive, then the singular point is invadable in at least one direction [25].

In one dimension the direction of evolutionary change is purely determined by the sign of the fitness gradient. As is evident from Equation (6), in many dimensions the direction of evolutionary change also depends on the mutational process. Convergence stability of the singular point is assessed via the Jacobian of the selection gradient, \mathbf{J} . It is obtained by the sum of the selection Hessian, \mathbf{H} , and the square matrix \mathbf{Q} , whose entries are

$$q_{ij} = \left. \frac{\partial^2 S(\mathbf{y}, \mathbf{x})}{\partial y_i \partial x_j} \right|_{\mathbf{y}=\mathbf{x}=\mathbf{x}^*}. \quad (8)$$

Three types of convergence stability are distinguished [25]. A singular point x^* is called *strong convergence stable* if it is a stable fixed point of Equation (6) for any mutational variance-covariance matrix $\mathbf{A}(\mathbf{x})$. This is the case when the symmetric part of \mathbf{J} is negative definite. *Weak convergence stability*, on the other hand, depends on the mutational processes of the resident type described in $\mathbf{A}(\mathbf{x})$. If the symmetric part of \mathbf{J} is indefinite, then convergence stability of the singular point depends on whether the matrix resulting from the product $\mathbf{A}(\mathbf{x})\mathbf{J}$ has all

eigenvalues with negative real parts. This means that convergence stability can occur only for a subset of all possible $A(\mathbf{x})$, although there is no guarantee that this subset is not empty. However, if the symmetric part of J is positive (semi)definite, then instability is guaranteed: the singular point is repelling in all directions. In many dimensions, a necessary but not sufficient condition for evolutionary branching is that the singular point is both convergence stable and invadable in at least one direction [25, 17]. Last, a singular point x^* is called *absolute convergence stable* when x^* is approached by all gradualistic paths that move uphill on a fitness landscape.

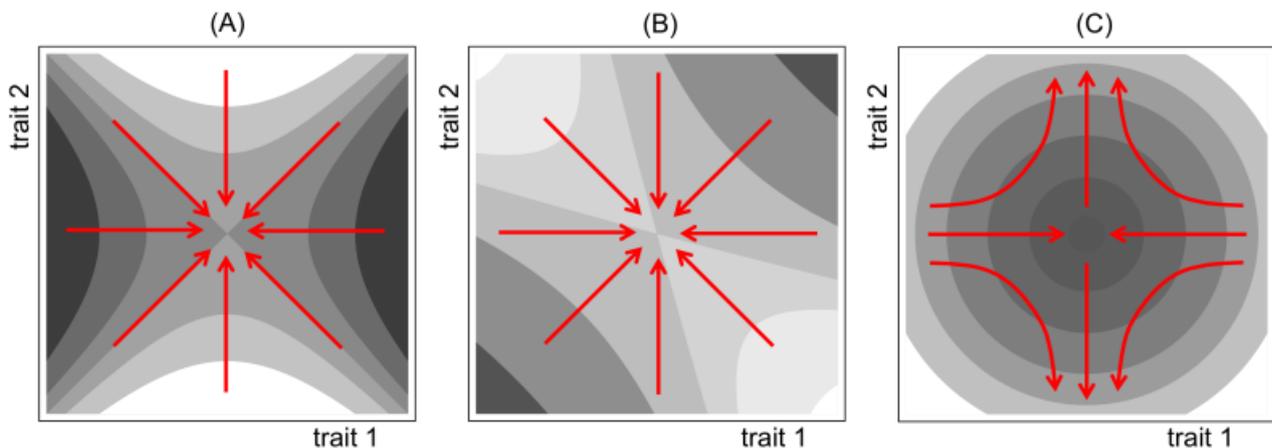


Figure 5: Trait co-evolution. Arrows indicate whether the point in the center – the singular point – is an attractor of the evolutionary dynamics, and the gray contours correspond to the fitness landscape for a rare mutant. Lighter contours correspond to higher values of $S(\mathbf{y}, \mathbf{x})$. In 5A, we have a continuously stable strategy in the direction of trait 1 that turns into an evolutionary branching point because the singular point is both attracting and invadable in the direction of trait 2. In 5B the singular point is evolutionary branching if the two traits co-evolve because it is invadable only in the direction where both traits change in concert. In 5C, the singular point will never be reached because it is a saddle point in the two dimensional trait space – attracting from one direction and repelling from another.

4 The multidimensional eye view: insights and conflicts

Evolutionary branching is a general and robust phenomenon in one-dimensional trait spaces, where it has been recognized as a major mechanism generating biological diversity [21, 13, 10,

37, 44, 34, 12, 18, 20, 30, 31]. However, to truly evaluate the significance of this phenomenon it is necessary to understand the impact of more realistically described systems on the potential for evolutionary branching – despite the fact that a multidimensional analysis is more mathematically challenging. A few studies analyzing higher dimensional trait spaces came out with findings that seem to point to two contradicting directions. Some found that increasing the dimensionality of trait space can facilitate evolutionary branching [14, 32, 39, 38, 15], and some found that, in fact, the potential for branching was diminished [3, 41, 39, 15]. The current state of affairs does not seem to provide a general understanding of the nature of this relationship.

4.1 Studies showing positive effects of dimensionality on branching

In a seminal paper Doebeli and Ispolatov [14] suggest that a positive correlation between the number of co-evolving traits and diversity is to be expected. In the corresponding one dimensional models, the frequency dependent component of selection needed to be stronger than the stabilizing component in order to enable diversification. But the authors show that, when organisms are described by multiple interacting traits that co-evolve, more directions exist in which the branching condition can be fulfilled, especially directions where several traits change simultaneously. What Doebeli and Ispolatov [14] find is not an effect of trait dimensionality alone, but of the *interactions* between these many traits – given that, without interactions, the requirements that frequency dependence be strong for maintenance of diversity are the same as for one dimensional cases.

Building on the work of Doebeli and Ispolatov [14], Svoldal et al. [38] analyze an explicit consumer-resource model where the fitness landscape results from the underlying mechanistic ecology described. The consumer species is characterized by an n -dimensional trait vector and feeds on an m -dimensional resource distribution. Feeding efficiency is determined by a key-hole mechanism where the feeding apparatus of the consumer has to match the properties of the resource item for consumption to be efficient. Again, in this realistically described model, the authors find a positive correlation between dimensionality of trait space in the consumer species and the potential to branch via a positive effect of the dimensionality of n and m on

the dominant eigenvalue of \mathbf{H} . Svardal et al. also derive two results based on random matrix approach: the first shows that adding nonzero off-diagonal entries to a diagonal matrix generally increases its dominant eigenvalue – i.e. adding trait dimensions either does not affect or facilitates branching by increasing the dominant eigenvalue of \mathbf{H} . The second result shows that for symmetric matrices whose entries are drawn from distributions over real numbers, the average dominant eigenvalue over all these matrices strictly increases with increasing dimensionality (Figure 5A). Since \mathbf{H} is a symmetric matrix, if it is also diagonal, this result is trivial. However, this result holds even when selection is constrained to be stabilizing in the direction of each phenotypic trait. So, increasing the dimensionality of trait space thus makes it more likely that at least one direction exists where the fitness landscape has a local minimum.

4.2 Studies showing negative effects of dimensionality on branching

Bolnick and Doebeli [3] show that adaptive lineage diversification is not the most likely outcome of disruptive selection, but that sexual dimorphism may also evolve – as they both require identical ecological conditions. The authors find that the potential for branching is greatly hampered when male and female traits are allowed to diverge. This occurs because evolution of sexual dimorphism can enable a population to evade strong competition and thus temper the force of frequency-dependent disruptive selection.

Then, Van Dooren et al. [41] confirm that, when allowing sexes to diverge, diversification is not likely to follow. Starting from a resource competition model that does not allow phenotypic differentiation between the sexes, they investigated whether evolutionary branching still occurs when the model allows sexual dimorphism. A singular point that is a branching point (convergence stable and invadable) in the original "constrained" model loses convergence stability when sexual dimorphism is permitted. The evolutionary dynamics thus leads away from the singular point. The authors conclude, echoing Bolnick and Doebeli [3], that evolutionary branching becomes much less likely when a population can take on either of two distinct phenotypes, lessening the impact of competition and thus reducing the intensity of frequency dependent selection. This seems to lend evidence to the case that, when increasing the number

of coevolving traits, the potential for evolutionary branching can be greatly hampered.

4.3 Studies showing mixed effects of dimensionality on branching

Svardal et al. [39], while investigating the co-evolution of two sources of phenotypic variation (genetic and plastic) in response to fluctuating selection, find that an evolutionary branching point can exist when two traits are allowed to co-evolve, while it does not exist if the traits evolve in isolation (also shown by Ravigné et al. [32]). This lends support to the idea that increasing dimensionality increases the potential for branching. However, the same study finds that a singular point that is branching in one dimension becomes convergence unstable in two dimensions. In the latter case, the positive eigenvalue of the Hessian influences the Jacobian to become unstable in one direction, that is, the singular point is a saddle point of the evolutionary dynamics – Figure 5C.

Debarré et al. [15] distinguish three different effects of trait dimensionality on stability of the Hessian and Jacobian. The first one, which they call combinatorial effect, is that in the absence of interactions between traits, stability conditions can be formulated for each trait separately. Therefore, if one increases the dimensionality of trait space, one also increases the odds that selection will be diversifying in the direction of at least one trait. This corresponds to a positive eigenvalue in one of the entries of \mathbf{H} – which is diagonal in the absence of interactions, and so its eigenvalues are its diagonal entries. Thus, loss of evolutionary stability becomes easier with increased dimensionality of trait space. However, the same argument applies to \mathbf{J} – the more traits, the more eigenvalues; and the more eigenvalues, the higher the probability that at least one will be positive. This relationship between trait dimensionality and positive eigenvalues is what Svardal et al. [38] showed as a trivial case of their second result, and is illustrated in Figure 5A.

The second effect, as shown in [38], is due to epistatic interactions – nonzero off-diagonal elements in \mathbf{H} . These increase the leading eigenvalue of \mathbf{H} , thus increasing the likelihood of loss of evolutionary stability and facilitating diversification. However, the caveat with epistatic

interactions is that it's possible they also make the eigenvalues of J positive, thus rendering the singular point convergence unstable (although J is usually too complex to make any general statements). This is along the same lines of what Van Dooren et al. [41] find: because of the effects that the selection Hessian can have on the Jacobian of the selection gradient, where the positive eigenvalues of the former contribute to instability in the latter, a potential branching point becomes repelling.

The third and last effect is due to trait correlations. Off-diagonal nonzero entries in the variance-covariance matrix A affect weak convergence stability. If J is a symmetric matrix, trait correlations do not affect negative definiteness of J . However, if J is asymmetric or has more than one species, then trait correlations increase the probability that it will have one positive eigenvalue, and so will not be convergence stable.

To summarize, Debarré et al. [15] show that the relationship between dimensionality and branching is not so simple and direct. This is due to the fact that when more traits coevolve, selection can be diversifying in there are more directions where selection can be diversifying, and also more directions where the equilibrium can be repelling.

5 What picture emerges?

In the preceding section I gave an overview of the current state of affairs when it comes to knowing how realistic representations of organisms in mathematical models affect the potential for evolutionary branching. It can be seen that the seemingly conflicting scenarios sprout from the relationship between the selection Hessian and the Jacobian of selection gradients. Since $J = H + Q$, the eigenvalues of H have some influence on the eigenvalues of J , albeit in a complicated manner [25]. Therefore, the results obtained in the studies cited above are not surprising at all, and it becomes clear that the specific scenario one finds depends on the details of each model.

Facilitation of evolutionary branching occurs when what used to be stabilizing selection in the direction of each trait in isolation turns into disruptive selection in directions where several traits evolve simultaneously – by turning at least one negative eigenvalue of the selection Hessian into a positive one [14, 15, 38], Figure 5A-B. On the other hand, hindrance occurs when a singular point becomes repelling in directions where traits co-evolve – by turning at least one negative eigenvalue of the Jacobian of the selection gradient into a positive one [41, 24, 39], Figure 5C.

Given that the Jacobian is influenced by the Hessian in complicated, non straightforward ways, it might be the case that deriving a general relationship between biological realism and evolutionary branching in terms of facilitation vs. hindrance will not be possible. But it is possible and necessary to refine our knowledge of this relationship by systematically investigating which specific conditions lead to which outcomes. Therefore, future endeavors should strive to model a wide range of specific eco-evolutionary scenarios in order to achieve a more fine-grained understanding of the branching of the tree of life.

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7 Quick glossary

Canonical equation	Differential equation approximating the trajectory of trait evolution with small mutational steps.
Continuously stable point	Singular point that is both convergence stable (attracting) and evolutionarily stable (uninvadable).
Convergence stable point	Singular point that is approached gradually by successive invasions, i.e. a attractor of evolutionary dynamics.
Evolutionarily singular point	Trait value at which the selection gradient vanishes.
Evolutionarily stable point	Singular point that cannot be invaded by any nearby mutants.
Evolutionary branching point	Singular point that is convergence stable (attracting) but not evolutionarily stable (invadable).
Invasion fitness	Per capita growth rate of a rare mutant in an environment where all relevant parameters are set by the resident.
Mutual invadability	Property of a set of strategies that have positive invasion fitness in respect to one another.
Selection gradient	Slope of invasion fitness at the resident's trait value. Gives information about the direction and speed of evolution.

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