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## Trait-Based Ecological and Eco-Evolutionary Theory

Christopher A. Klausmeier, Colin T. Kremer, Thomas Koffel

### 1. Overview of Trait-Based Ecology and Evolution

#### 1.1. Why trait-based ecology?

Ecological systems are complex, consisting of a diversity of organisms whose growth, reproduction, and interactions are often nonlinear. Furthermore, these processes occur over multiple scales of organization and in environments that are heterogeneous in space and time. Theoretical ecologists have long pursued ways to simplify this complexity by identifying, describing, and exploring the essential features that drive ecological processes and patterns (Levin 1992). One such approach, trait-based ecology, offers a potent way of studying the theoretical underpinnings of diversity, while balancing reductionism and reality. This emerging paradigm unites new and old ideas behind a common focus: that by reducing our representation of individuals, populations, or species to their most essential characteristics — functional traits — we can better understand ecological systems.

Trait-based approaches cut across organization scales from the behavioral and physiological up to the population, community, and ecosystem levels, making it possible to study a range of fundamental questions. For example, the performance of a population of individuals within a given ecological setting might be revealed by considering the traits of an average individual, such as its life history, behavior, and physiology. Similarly, the distribution of an entire species across a range of environments might be understood by considering its mean trait values, across individuals and populations (although trait variation also matters; Violle *et al.* 2012, Enquist *et al.* 2015). Traits can also be used to characterize a range of interactions between species, yielding insights into coexistence, trophic interactions, and ultimately the diversity and composition of entire communities. In turn, representing whole communities using features of their collective trait distributions, rather than focusing in detail on the identity of their constituent species, can reveal general patterns of succession (e.g. Terseleer *et al.* 2014) and the influence of climate (e.g. Wiczyński *et al.* 2018). Critical properties of ecosystems (productivity, stability, *etc.*) may also be related to the traits (or functions) of the communities they support (e.g. Díaz and Cabido 2001, Roscher *et al.* 2012, Polley *et al.* 2013). Finally, trait-based approaches have the potential to integrate ecological and evolutionary perspectives, due to their common focus on functional traits (or phenotypes) and measures of fitness. This makes it possible to consider both the ecological consequences of evolutionary trait change and the capacity of ecological forces to impose selection and drive evolution.

Trait-based approaches are valuable to ecological theory, offering both qualitative and quantitative insights. Qualitatively, trait-based studies can uncover the mechanisms that drive ecological processes, informing the structure of the equations used to develop a model or theory. Quantitatively, these studies also provide the parameters of equations by measuring rates, efficiencies, and other key traits. Consequently, trait-based theories are often inherently mechanistic, due to their focus on function; this contrasts with other theoretical techniques for modeling diverse communities such as constructing random community matrices or interaction networks (May 2001, Allesina and Tang 2012, Barbier *et al.* 2018). To avoid biologically nonsensical results, many ecological theories invoke one or more tradeoffs (Kneitel and Chase 2004). Often these tradeoffs represent reasonable assumptions, which may nevertheless lack a

strong empirical foundation. Trait-based studies have the potential to provide new and quantitative insights into the tradeoffs that constrain the strategies used when competing for resources, avoiding predation, timing reproduction, *etc.* (Edwards *et al.* 2011). Furthermore, in an era where ecologists are increasingly challenged to quantitatively predict how species, communities, and ecosystems will respond to environmental change, a focus on species traits is essential. Trait-based approaches are being used to anticipate shifts in species distributions, community composition, and ecosystem function driven by environmental change (Suding *et al.* 2008, Thomas *et al.* 2012). They can also be used to predict which species are likely to become harmful invaders outside their native ranges (Van Kleunen *et al.* 2010, Drenovsky *et al.* 2012), and to identify alternative targets for conservation, such as focusing on the preservation of functional biodiversity. Collectively, these examples give an indication of the value of trait-based approaches both for advancing basic theory as well as testing and applying theory in real ecological systems.

### 1.2. What are traits?

*Traits* can be defined as measurable properties of individual organisms; we are particularly interested in *functional traits*, those that affect performance and ultimately fitness (McGill *et al.* 2006, Violle *et al.* 2007). There are many different kinds of traits, reflecting the chemical composition, physiology, morphology, genetics, and behavior of organisms. Traits determine how a given individual functions within its environment (*e.g.* its capacity to tolerate temperature or toxins) as well as how it interacts with other individuals or species (*e.g.* its ability to compete for resources or escape from predators). Traits may characterize how an organism is affected by its environment (often called ‘response’ traits), how it influences its environment (‘effect’ traits), or both (Díaz and Cabido 2001; Lavorel and Garnier 2002; Violle *et al.* 2007). Mathematically, traits can be characterized as discrete, categorical, continuous, or even function-valued (Gomulkiewicz *et al.* 2018).

Numerous reviews have identified the functional traits most relevant to different groups of organisms (*e.g.* phytoplankton, Litchman and Klausmeier 2008; zooplankton, Litchman *et al.* 2013; plants, Westoby *et al.* 2002, Reich *et al.* 2003; insects, Poff *et al.* 2006), while considering relationships among traits, and how traits inform our understanding of ecology. Some of these studies categorize traits according to their type (life history, behavioral, physiological, morphological) and ecological function (reproduction, resource acquisition, predator avoidance). Given the vast number of possible traits, it is often useful to organize them into hierarchies, recognizing that the value of ‘high level’ traits is determined by combinations of a large number of lower level traits. For example, while size might strongly influence an individual’s fitness, size itself is the product of other traits, ranging from how an individual develops and forages, to the level of individual genes. Establishing the relationships between traits across such hierarchies, including eventually bridging the genotype/phenotype gap, remains an active and important area of research.

### 1.3. Historical survey of trait-based theories

The foundations of trait-based ecology long predate its emergence as an identifiable paradigm. Even the very earliest attempts to use mathematics to describe and study ecological processes invoked relationships that depended on parameters representing the traits of

populations and species. For example, logistic growth (Verhulst 1845) depends on a population's intrinsic growth rate and strength of intraspecific competition, and predatory-prey dynamics (Lotka 1920, Volterra 1926) are governed by traits including the growth rate of the prey, and the attack rate, conversion efficiency, and mortality rate of the predator. Corresponding efforts to parameterize such models engaged empiricists in quantifying these, and many other traits across different species and under different conditions. However, these early approaches focused on population dynamics, using traits as parameters but not state variables themselves.

These traditional ecological models lay a solid foundation for trait-based approaches, by linking model parameters with the traits of organisms. Trait-based approaches take this one step further, by focusing on traits as key model outputs rather than just inputs. That is, traits are not fixed parameters but dynamic variables subject to change, typically by some adaptive processes. This opens up a whole new range of questions that can be addressed.

*Optimization theory* was one of the first trait-based theories in ecology and evolution (Parker and Maynard Smith 1990), with many notable, broad fields of application. *Life history theory* addresses questions such as optimal clutch size and the timing of life history events, assuming trade-offs between demographic traits such as survival, growth and reproduction (Stearns 1992, Roff 2002). *r/K selection* is an example linking suites of traits to the environment (MacArthur and Wilson 1967). *Optimal foraging theory* is another a well-developed field (Stephens and Krebs 1986), where traits are the effort spent foraging on different resources. These traits are typically assumed to be optimized on a rapid, behavioral timescale. Classic results include the marginal value theorem for patch use (Charnov 1976), the zero-one rule for substitutable resources (Emlen 1966), and the  $\mu/f$  rule for balancing foraging gains and predator risk (Gilliam and Fraser 1987). *Eco-physiology* addresses resource allocation to different physiological systems (e.g., Bazzaz and Grace 1997; Klausmeier *et al.* 2004).

Although optimization theory is a central organizing theory in many areas of ecology and evolution, it has been criticized on various grounds (summarized in Maynard Smith 1978). One limitation of optimality approaches is that they assume that the payoff depends only on the strategy played by an individual. However, for ecological interactions that occur within and between species, the payoff of a strategy often depends on what strategy other individuals are playing. *Game theory* was designed to investigate such situations, originally in economics (Von Neumann and Morgenstern 1944, Nash 1951) and later imported to biology (Maynard Smith and Price 1973) where it became a standard approach to studying animal behavior (Maynard Smith 1982). The concept of an optimum strategy is replaced by the *evolutionarily stable strategy* (ESS), a strategy that cannot be improved on once it is adopted by an entire population. Many applications of game theory in behavioral ecology consider a discrete set of strategies, so the payoffs can be assembled in a matrix, but continuous strategy spaces are also possible.

Another body of trait-based theory, concerning competition for a spectrum of substitutable resources, dominated community ecology theory in the 1970s. Species differ in their resource utilization curves, which are related to a trait such as body or beak size, averaged at the species level. This underlying mechanistic model is then translated into a Lotka-Volterra competition model, where a species' carrying capacity depends on its trait and the competition coefficients depend on the difference in species' traits. MacArthur and Levins (1967) first used

such a model to examine *limiting similarity*: how similar two resident species must be to prevent an intermediate species from invading. This approach was soon extended to a large number of species evenly spaced along the trait axis. Roughgarden (1972, 1979) showed that an unlimited number of species can coexist in an idealized deterministic setting, but May and MacArthur (1972) found a limit to diversity in randomly varying environments. This result was criticized on mathematical (Turelli 1978) and ecological grounds (Abrams 1983), and the theory of limiting similarity fell out of fashion by the 1980s. Despite this history, these one-dimensional Lotka-Volterra models are still widely used in trait-based eco-evolutionary modeling. We now know much more about the conditions that lead to continuous species packing versus a discrete number of coexisting species (Barabás *et al.* 2012).

One reaction to the disenchantment with this niche-based Lotka-Volterra theory was a shift to more mechanistic models of competition that explicitly include the resources for which species compete (Tilman 1982), although, the niche-based Lotka-Volterra was originally formulated as an explicit resource-consumer model (MacArthur 1970, Chesson 1990). Extended to include apparent competition through shared predators and stressors, this *contemporary niche theory* employs a graphical approach to determine community structure based on zero net growth isoclines (ZNGIs), which summarize the response of organisms to the environment, and impact vectors, which summarize the effect of organisms on the environment (Chase and Leibold 2003). Because these models are more mechanistic, the species parameters have direct ecological meaning, so can be considered traits. A common form of trait-based analysis of these models involves depicting a large number of species' ZNGIs and impact vectors, which can be used to determine community structure along environmental gradients (Tilman 1982, Chase and Leibold 2003). Recently we have extended this approach using ZNGI and impact vector envelopes to consider a continuum of strategies (Koffel *et al.* 2016). However, these graphical approaches restrict the number of limiting factors to two or three, capping the diversity that can emerge.

In the late 1980s and 1990s, two independent groups — one American (Brown and Vincent 1987), one European (Metz *et al.* 1996) — proposed a trait-based theoretical framework that allows for the emergence of community structure, termed *adaptive dynamics* (Geritz *et al.* 1998). These approaches combine ideas from evolutionary game theory and community ecology. In particular, they show how game theory's payoff can be identified with Darwinian fitness, which is described as the *per capita* population growth rate in a community ecological model. This general formulation provided analytical tools that could be applied to arbitrary ecological interactions (*i.e.* not restricted to Lotka-Volterra models), which led to a flood of applications (see section 2.3). The original formulation of adaptive dynamics makes a number of restrictive assumptions, such as a separation of time scales between ecology and evolution, small mutations, and asexual populations; however, it can be seen as a particular case within a constellation of closely related theoretical frameworks (Abrams 2001; section 3).

One other framework from the 1980s and 1990s worth mentioning is that of *community assembly theory*. In this purely ecological framework, species from a finite or infinite regional species pool are repeatedly introduced to a local community (Post and Pimm 1983, Rummel and Roughgarden 1985, Law and Morton 1993, Morton and Law 1997). Upon successful invasion, the new state of the community is computed and another random species is introduced from the regional species pool. Three outcomes are possible: the community is

uninvasible, a recurrent assembly cycle occurs, or community assembly continues indefinitely along different trajectories (Morton and Law 1997). Furthermore, alternative outcomes are possible for a given set of parameters (Law and Morton 1993). Although any model of species interactions could be used, Lotka-Volterra models are typical; many applications employ trait-based models of competition (Rummel and Roughgarden 1985) or food web assembly (Morton and Law 1997) to define species interactions. The community assembly framework shares many similarities with adaptive dynamics — trait-based formulations of interactions, use of invasion criteria, separation of time scales between invasions, and uninvasible states as a long-term outcome — but these literatures have remained largely separate.

#### 1.4. Overview of rest of chapter

Clearly, there is a rich history of trait-based theoretical approaches in ecology and evolution. In the rest of this chapter, we describe how trait-based models are set up and analyzed from the perspective of adaptive dynamics, and survey applications (section 2). Next, we discuss other trait-based modeling frameworks and the connections between them (section 3). We then consider the extension of these frameworks to multiple traits and spatial and temporal heterogeneity (section 4). Finally, we conclude in section 5 by considering directions for future research.

## 2. Trait-Based Theory - Basic Ideas

In this section we outline the basic principles of trait-based theory, considering both density-independent and density-dependent models, feedbacks between ecological / environmental conditions and trait values, and how optimization and evolutionary approaches offer insights into the dynamics and equilibria of such models. Finally, we conclude by describing a range of phenomena uncovered by applying trait-based theory.

Before we start, some words about terminology. With their focus on functional traits, trait-based approaches are, by design, phenotypic approaches. The hierarchical level at which trait variation occurs — within-individual plasticity, within-species genetic variation, or between-species differentiation — is a secondary concern and often ignored. While this is a strength of the approach because it can allow greater generality, it can lead to confusing use of terminology. Here, we will use the term *strategy* to refer to the trait values of an individual, or of a population or species when intraspecific trait variation is negligible. For frameworks that are explicitly ecological, we refer to different species as such, but for more general frameworks we use the term *populations*.

### 2.1. Density-independent models with traits and optimization theory

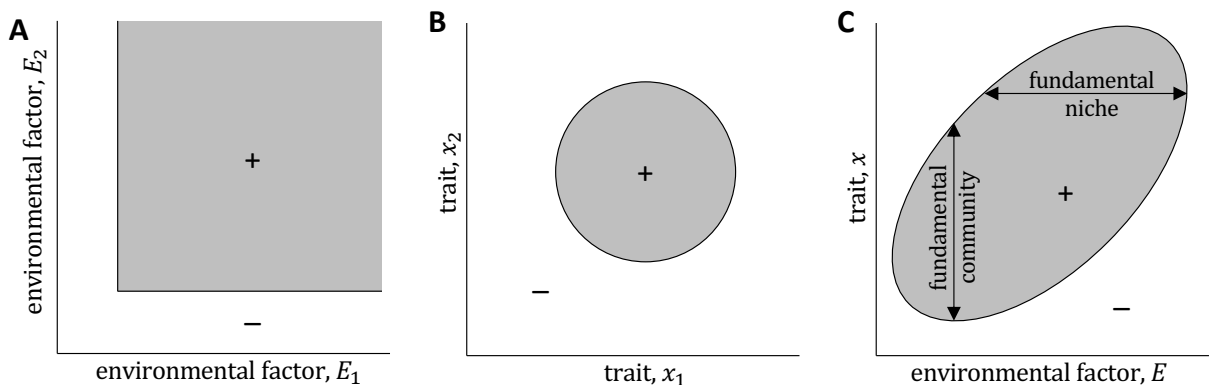
Exponential growth has been called the first law of population dynamics (Turchin 2001, Pásztor *et al.* 2016). Such density-independent models form the basis of the simplest approach to trait-based modeling — optimization theory — and are fundamental to understanding more realistic density-dependent models. We begin with the simplest case of an unstructured population  $i$  in a constant environment in continuous time, with population density  $N_i$  and growth rate  $r_i$ :

$$\frac{dN_i}{dt} = r_i N_i \quad (1)$$

The solution of this equation is  $N_i(t) = N_i(0)e^{r_it}$ , which approaches zero if  $r_i < 0$  and grows to infinity if  $r_i > 0$  (assuming no dispersal limitation, that is  $N_i(0) > 0$ ). Equilibrium is possible only when  $r_i = 0$ , which is infinitely unlikely in the absence of any density-dependent stabilizing mechanism.

Simple as exponential growth may be, we can begin to get ecological insights by considering how a population's growth rate  $r_i(\vec{x}_i; \vec{E})$  depends on its traits  $\vec{x}_i$  and the environment  $\vec{E}$  (Geritz *et al.* 1998). In general, the environment is a multidimensional vector that represents all of the abiotic and biotic factors that affect a population's growth rate, such as resource levels, temperature, and the density of directly interacting species (assumed to be constant in the density-independent case). How  $r_i$  depends on traits and the environment is the domain of functional and physiological ecology and is a key element in developing mechanistic trait-based models, including species distribution models (Kearney and Porter 2009).

The critical values of the traits and environmental factors where  $r_i(\vec{x}_i; \vec{E}) = 0$  separate population growth from extinction (Maguire 1973). This can be easily visualized in two dimensions (*e.g.*, two environmental variables, two traits, or one of each), which we call Zero Invasion Plots or ZIPs (Fig. 1). Fig. 1A illustrates the classical case of a population with fixed trait values that requires two essential resources, such as nitrogen and phosphorus for plants, so that  $\vec{E} = (R_1, R_2)$ . Both resources are required for growth, which leads to the L-shaped Zero Net Growth Isocline or ZNGI (Tilman 1982). Fig. 1B shows a hypothetical situation for a fixed environment where positive growth occurs for a range of values of each trait. This region also depends on an interaction between these traits (such that the viable range of trait 1 depends on the value of trait 2 and *vice versa*). Fig. 1C shows the interaction between a single trait and one environmental factor. A horizontal slice through this figure determines the fundamental niche of a population with particular trait values. A vertical slice determines what we call the *fundamental community* for a particular environment: species with trait values outside the fundamental community cannot persist even in isolation, so would not be expected to occur absent facilitation.



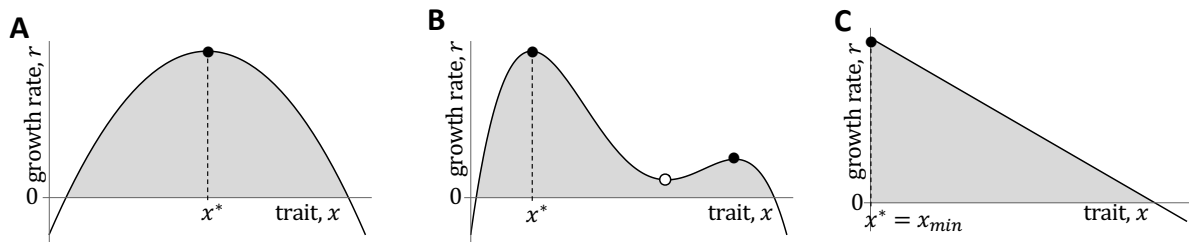
**Figure 1.** Zero Invasion Plots. **A)** Two environmental factors (a ZNGI). **B)** Two traits. **C)** One environmental factor and one trait. Gray shading denotes positive fitness.

Now, consider multiple populations, which could represent different species (or, alternatively, different strategies within a species) inhabiting the same environment, governed by eq. (1), and growing (*i.e.*,  $r_i > 0$ ). Although these populations do not interact and each has the potential to grow to infinity due to the lack of density dependence, we can still determine the outcome of “competition” among these populations by considering the relative abundance of each population,  $p_i = n_i / \sum_j n_j$ . Using the quotient rule, we find the dynamics of  $p_i$  to be

$$\frac{dp_i}{dt} = p_i(r_i - \sum_j r_j p_j) = p_i(r_i - \bar{r}), \quad (2)$$

where  $\bar{r}$  is the abundance-weighted average growth rate. This is known as the replicator equation (Hofbauer and Sigmund 1998). As can be seen from the second form of eq. (2), a population  $i$  with an above-average growth rate ( $r_i > \bar{r}$ ) increases in relative abundance and one with a below-average growth rate decreases. Thus, in the long term, the population with the highest growth rate will dominate the community ( $p_i \rightarrow 1$ ), while the relative abundance of all others will decline to zero. This justifies the use of the word *fitness* as a synonym for the *per capita* growth rate,  $r_i$ . If multiple populations have equal fitness, we say they are *neutral* because their relative abundance is fixed only by initial conditions.

Instead of a finite number of populations, we now consider a continuum of populations, ordered by their strategy  $x$ , which also determines their fitness,  $r(x)$ . Generalizing the results from the replicator equation (2), we know that the population with the strategy conveying the greatest fitness will dominate the community in the long term. We can use elementary calculus to find the optimal strategy,  $x^*$ , which maximizes fitness given  $r(x)$ . If  $x$  is one-dimensional, we find the maximum by setting the *fitness gradient*,  $\frac{dr}{dx}$ , equal to zero and solving for  $x$ . To be a local maximum, we require the second derivative of fitness to be negative,  $\frac{d^2r}{dx^2} < 0$  (Fig. 2A). Since there can be multiple local maxima, we have to compare the fitness of all local optima as well as at the ends of the trait space to find the global optimum  $x^*$  (Fig. 2B-C).



**Figure 2.** Finding local and global maxima on fitness landscapes. **A)** A single, global optimum. **B)** Two local optima separated by a fitness minimum. **C)** A boundary optimum.

So far, we have focused on continuous-time models with *unstructured populations*, which can be described by a single variable such as population size or density. However, the theory of *structured populations* (those with *e.g.* age-, stage-, or size-structure) is well developed, and provides ways to calculate the asymptotic population growth rate  $r$  once a stable population structure has been reached. In a discrete-time matrix model, it is the logarithm of the dominant eigenvalue of the Leslie/Lefkovich matrix (Caswell 2001). Extensions to temporally variable environments also exist: Floquet exponents for periodic systems (Klausmeier 2008) and Lyapunov exponents for aperiodic systems (Metz *et al.* 1992). Thus, the



population growth rate  $r$  can be optimized while accounting for all the biological processes contributing to a population's success, such as individual growth, survival, and reproduction.

## 2.2. Density-dependent models with traits

### 2.2.1. Density dependence and limiting factors

It has long been recognized that at least some *per capita* vital rates must depend on population density for populations to not to grow to infinity (Turchin 2001). While this density dependence is often modeled as a direct effect of density on *per capita* growth rate, as in the logistic equation, it is often useful to explicitly consider the limiting factors such as resources or predators that mediate density dependence (Chase and Leibold 2003, Meszena *et al.* 2006). One important consequence of this environmental feedback loop is the *competitive exclusion principle*: no more species can coexist at equilibrium than there are shared limiting factors (Levin 1970). This sets an upper limit on the diversity that can be maintained in a community, a limit that remains valid in trait-based models.

In particular, when there is only one limiting factor, such as a resource  $R$ , stable coexistence is impossible and a single population will outcompete all others. The break-even resource level  $R^*$  of a population  $i$ , where its net growth  $g_i = 0$ , is a simple metric that identifies the best competitor: the population with the lowest  $R^*$  will exclude all others. This is known as the  $R^*$ -rule (Tilman 1982). Thus  $R^*$  combines various physiological parameters into a single metric of competitive ability. In a trait-based setting, the  $R^*$ -rule provides a "pessimization" principle analogous to the optimization principles applied to fitness above (Metz *et al.* 2008). When  $R^*$  is expressed as a function of traits, calculus can again be used to minimize  $R^*$  and identify the optimal trait values for a given environment (Klausmeier *et al.* 2004).

If species interacted only through a single limiting factor, ecological communities would be much easier to understand, yet lack diversity, rendering them far less interesting. Luckily this is not the case. When there is more than one limiting factor and populations have differential responses and effects on those factors, then stable coexistence becomes a theoretical possibility. The prototypical species-based competition model is the Lotka-Volterra model, which can be written as

$$\begin{cases} \frac{dN_1}{dt} = (r_1 - \alpha_{11}N_1 - a_{12}N_2)N_1 = g_1N_1 \\ \frac{dN_2}{dt} = (r_2 - \alpha_{21}N_1 - a_{22}N_2)N_2 = g_2N_2 \end{cases} \quad (3)$$

where  $r_i$  are maximum growth rates and  $\alpha_{ii}$  and  $\alpha_{ij}$  are intra- and interspecific competition coefficients, respectively. The five possible outcomes of competition are: i) species 1 outcompetes 2, ii) species 2 outcompetes 1, iii) species 1 and 2 coexist, iv) either species 1 or 2 excludes the other depending on initial conditions (*founder control*), or v) neutral coexistence. Note that in eq. (3), we have introduced  $g_i$  to represent the *per capita* growth rate (fitness) of a population, which now combines the maximum exponential growth rate,  $r$ , with density dependence.

### 2.2.2. Invasion analysis

*Invasion analysis* is a powerful approach to understanding coexistence between two populations (Chesson 2000). The idea is to ask whether each population (termed the *invader*)

can invade a monoculture of the other (termed the *resident*) at its equilibrium or other long-term attractor. The invader is assumed to be sufficiently rare that it has no effect on its own per capita growth rate or the resident's. This results in density-independent growth of the invader, which is characterized by its *invasion fitness*,  $g_{\text{inv}}(E_{\text{res}})$ . Here the resident at its attractor determines the environment,  $E_{\text{res}}$ , experienced by the invader (consisting of limiting factors, possibly including its own density). Negative invasion fitness means that the invasion fails, while positive invasion fitness means that it succeeds. If one population has positive invasion fitness but the other has negative, then the first excludes the second (Lotka-Volterra cases i-ii); if both populations have negative invasion fitness, there is founder control (Lotka-Volterra case iv). Finally, if each population has a positive invasion fitness (*i.e.* they are mutually able to invade), then we say that the two populations *stably coexist* (as in Lotka-Volterra case iii). However, because invasion fitness focuses on the boundaries of the phase space, it does not give us any information on the nature of coexistence in this mutual invasibility case.

The main advantage of invasion analysis is that it is easier to calculate invasion rates than to solve for the coexistence attractor and determine its stability. However, invasion analysis has a few potential shortcomings. First, if there are multiple coexistence equilibria, then the lack of mutual invasibility does not imply that coexistence is impossible (Namba and Takahashi 1993, Priklopil 2012). However, it can be argued that such locally stable coexistence would be vulnerable to stochastic events and that mutual invasibility is more relevant to natural systems. Second, when the resident has multiple attractors, a positive invasion rate does not necessarily imply that the invader persists. Instead the invader can shift the resident from one of its attractors to the other, which then repels the invader, termed the “resident strikes back” scenario (Mylius and Diekmann 2001). Third, it is unclear how to extend invasion analysis to more than two species (Saavedra *et al.* 2017). Nonetheless, invasion analysis remains a key tool for understanding competition and forms the basis of many trait-based eco-evolutionary modeling approaches (see below).

### 2.2.3. How to set up density-dependent trait-based models

Having discussed species-based density-dependent models above, let us now describe how to set up a trait-based model in four easy steps, focusing on non-structured populations for simplicity. First, start with a mechanistic species-based model and identify groups of populations that are functionally similar, which we call *guilds*. Populations within a guild share the same fitness function, which will depend on the same trait(s), but specific trait values may differ between populations. If two populations do have identical trait values, or strategies, they will be selectively neutral (*e.g.* Lotka-Volterra case v). As an example, one might model predators and prey as two separate guilds (although this decision is part of the art of modeling). Let  $\mathcal{G}$  be the number of guilds.

Second, generalize the model to encompass  $\mathcal{N}_G$  populations in guild  $G$ , indexed by subscripts. For example, let  $N_{G,i}$  be the density of the population with the  $i^{\text{th}}$  strategy in guild  $G$ . Any terms that represent interactions between populations or between populations and environmental factors should be replaced by a sum over populations, making no distinction between intra- and inter-specific interactions.

Third, make some model parameters functions of traits (this is the identity function if those parameters are directly considered traits). Together, the model then consists of a set of

differential equations of the form  $\frac{dN_{G,i}}{dt} = g_G(x_{G,i}; \vec{E}(\vec{N}, \vec{x}))N_{G,i}$ , one for each population in each guild. Note that the fitness function  $g_G$  of a particular guild now depends on the strategy of the focal population,  $x_{G,i}$ , as well as environmental factors  $\vec{E}$ . These in turn depend on the strategies and densities of the rest of the community. Specifically,  $\vec{x} = (\vec{x}_1, \vec{x}_2, \dots, \vec{x}_G)$  and  $\vec{x}_G = (x_{G,1}, x_{G,2}, \dots, x_{G,N_G})$  describe the set of all traits across guilds, and across populations/strategies within a guild, respectively. Densities are described similarly as  $\vec{N} = (\vec{N}_1, \vec{N}_2, \dots, \vec{N}_G)$  and  $\vec{N}_G = (N_{G,1}, N_{G,2}, \dots, N_{G,N_G})$ . See Boxes 1 and 2 for examples of how to set up trait-based models.

The final step in setting up a trait-based model is to define a source of trait variation. This choice largely distinguishes various trait-based modeling frameworks, which we compare in section 3. For pedagogical reasons, we will describe adaptive dynamics (which assumes variation arises from small, infrequent mutations) and adaptive statics (adaptive dynamics at equilibrium, without the assumption of small mutations) below; however, different trait-based approaches often give similar results (see section 3).

It is important to keep in mind that there is usually no unique way of deriving a trait-based model from a species-based one. All of the four steps above (identifying guilds, generalizing to multiple populations, making parameters functions of traits, and defining a source of variation) are ultimately determined by the ecological mechanisms identified as relevant by the modeler in that particular context. For example, a trait-based model designed to study the evolution of cannibalism would look different from the competition model derived in Box 1, even if both arose from the same single-population model. Similarly, trait-based models studying the emergence of food webs might lump prey and predators into a single guild, unlike Box 2.

**Box 1: Trait-Based Lotka-Volterra Competition**

A classic example of a trait-based model arises from the Lotka-Volterra competition model. In it, there is a single guild of competitors and no explicit environmental factors aside from the abundance of competitors. Start with the single-population logistic equation

$$\frac{dN}{dt} = (r - \alpha N)N$$

To make it into a trait-based model, we add subscripts for each population  $i$ , sum interactions over strategies  $j = 1, \dots, \mathcal{N}$ , and make model parameters  $r = r(x_i)$  and  $\alpha = \alpha(x_i, x_j)$  functions of the focal population's trait  $x_i$  and the interacting population's trait  $x_j$ . Together, these changes result in:

$$\frac{dN_i}{dt} = \left( r(x_i) - \sum_{j=1}^{\mathcal{N}} \alpha(x_i, x_j)N_j \right) N_i = g(x_i; \vec{x}, \vec{N})N_i$$

For simplicity, we drop the guild subscript and the explicit consideration of the environment  $\vec{E}$  from the general formulation in section 2.2.3. It is commonly assumed that the maximum growth rate  $r$  is a unimodal function of  $x$  and that  $\alpha$ , the strength of competition (competition kernel), declines to zero as a function of the difference in the strategies of the focal and interacting populations. Two functions that satisfy these assumptions are the quadratic  $r(x) =$

$1 - x^2$  and the Gaussian  $\alpha(x_i, x_j) = \exp \left[ -(x_i - x_j)^2 / \sigma^2 \right]$ , where  $\sigma$  controls the width of competition kernel (Fig. 3).

Motivated by the seminal work of MacArthur and Levins (1967), trait-based Lotka-Volterra models have been used to investigate the conditions under which such models lead to the coexistence of finitely many species with distinct trait values or a continuum of species (Barabás *et al.* 2012).

**Box 2: Trait-Based Predator-Prey Interactions**

As a more complicated example of how to set up a trait-based model, consider predator-prey interactions. We begin with a classic predator-prey model, the Rosenzweig-MacArthur model (Rosenzweig and MacArthur 1963), where a prey with abundance  $N$  is consumed by a predator with abundance  $P$ :

$$\begin{aligned} \frac{dN}{dt} &= (r - \alpha N)N - \frac{aN}{1 + haN}P \\ \frac{dP}{dt} &= \frac{eaN}{1 + haN}P - mP \end{aligned}$$

The prey grows at an intrinsic rate  $r$  and self-regulates through a competition coefficient  $\alpha$ . The predator consumes the prey through a type II functional response with attack rate  $a$  and handling time  $h$ , and converts prey abundance into predator abundance with efficiency  $e$ . Finally,  $m$  sets the mortality rate of the predator.

To convert the above model into a trait-based model, we first need to identify the guilds at play. A natural choice here consists of introducing two guilds: the prey guild and the predator guild. Their abundances, generalized to multiple populations, are respectively denoted  $N_i$  with  $i = 1, \dots, N_N$  and  $P_j$ , with  $j = 1, \dots, N_P$ . Let the fitness function of the prey and the predator depend on traits  $x$  and  $y$ , respectively. We can then write:

$$\begin{aligned} \frac{dN_i}{dt} &= \left( r(x_i) - \sum_{j=1}^{N_N} \alpha(x_i, x_j)N_j - \sum_{j=1}^{N_P} \frac{a(x_i, y_j)}{1 + \sum_{k=1}^{N_N} h(x_k, y_j)a(x_k, y_j)N_k} P_j \right) N_i \\ &= g_N(x_i; \vec{x}, \vec{y}, \vec{N}, \vec{P})N_i \\ \frac{dP_j}{dt} &= \left( \sum_{i=1}^{N_N} \frac{e(x_i, y_j)a(x_i, y_j)N_i}{1 + \sum_{k=1}^{N_N} h(x_k, y_j)a(x_k, y_j)N_k} - m(y_j) \right) P_j = g_P(y_j; \vec{x}, \vec{y}, \vec{N}, \vec{P})P_j \end{aligned}$$

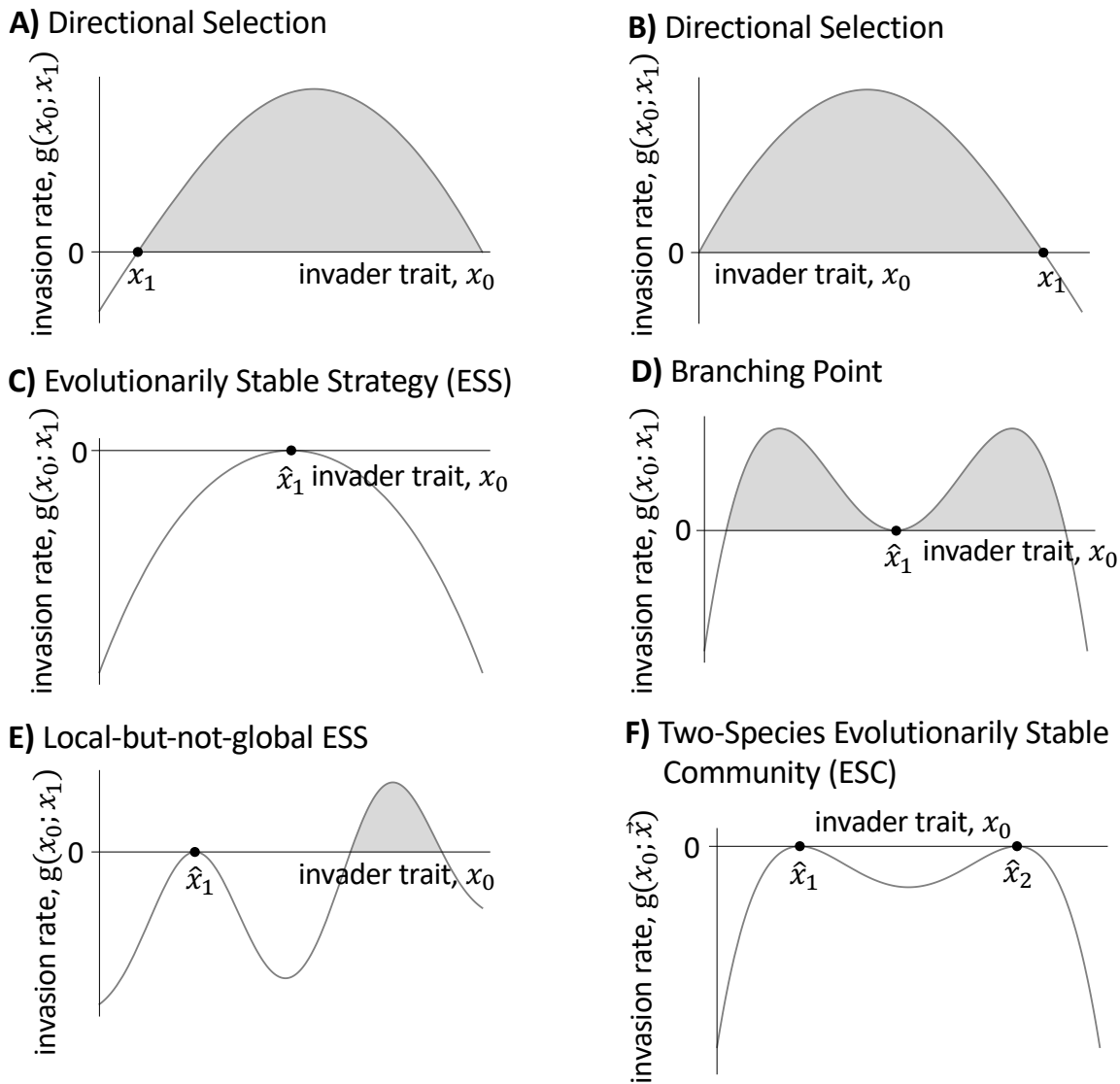
As in the Lotka-Volterra competition model in Box 1, prey growth rate  $r(x_i)$  depends on the focal population's trait value and density-dependence  $\alpha(x_i, x_j)$  depends on the trait values of the focal and interacting prey populations. The predator's attack rate  $a(x_i, y_j)$ , handling time  $h(x_k, y_j)$ , and conversion efficiency  $e(x_i, y_j)$  all depend on the trait values of the predator and prey involved. Note that there are multiple interactions in this model that have been replaced by summations. The first summation in the prey equation adds up competition between prey populations; the second summation adds up predation by different predator populations; and the third summation in the denominator of the functional response adds up time predator  $j$  spends handling different prey. Finally, the outer summation in the predator equation adds up energetic gain from different prey populations.

#### 2.2.4. Invasion analysis of trait-based models

Having defined a trait-based model, how can we analyze it? For simplicity, we will consider a single guild with a single trait here. Begin with a monomorphic resident population with strategy  $x_1$  and find its ecological attractor (assumed here to be an equilibrium for simplicity) and the corresponding environment  $\hat{E}(x_1)$ , such that  $g(x_1; \hat{E}(x_1)) = 0$ . Now consider the fate of a rare population with a different strategy  $x_0$  by calculating its invasion fitness when invading the resident,  $g(x_0; \hat{E}(x_1))$ . As described above, invasion succeeds if  $g(x_0; \hat{E}(x_1)) > 0$  and fails if  $g(x_0; \hat{E}(x_1)) < 0$ . If the new strategy is quite similar to the existing one, then successful invasion implies replacement of the previous resident (Geritz *et al.* 2002), except at special points described below. This process is then repeated to generate a “trait substitution process”. The *fitness gradient*,  $\partial g / \partial x_0 |_{x_0=x_1}$ , measures *directional selection* on a resident, given its strategy: if  $\partial g / \partial x_0 > 0$  then the trait evolves towards larger values (Fig. 3A) and if  $\partial g / \partial x_0 < 0$  then it evolves towards smaller values (Fig. 3B). We will call a trait value or strategy  $\hat{x}_1$  where directional selection disappears ( $\partial g / \partial x_0 = 0$ ) an *evolutionary equilibrium*, also known as a singular strategy (Geritz *et al.* 1998).

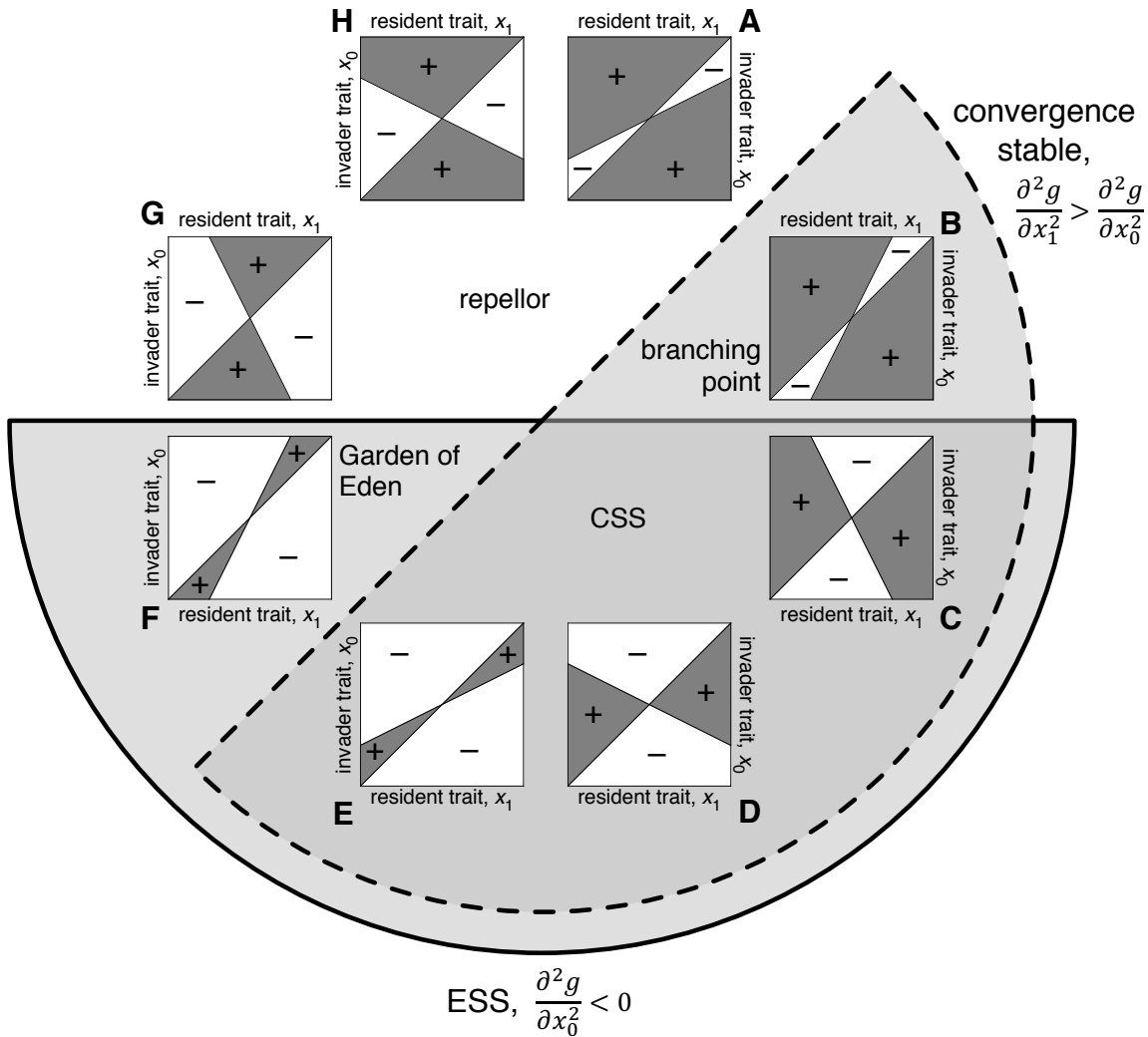
An evolutionary equilibrium is called a (global) *evolutionarily stable strategy (ESS)* if no other strategy can invade it. As in optimization models, an evolutionary equilibrium can be either a fitness maximum, and hence at least locally evolutionarily stable, if  $\partial^2 g / \partial x_0^2 |_{x_0=x_1} < 0$  (Fig. 3C), or a fitness minimum, if  $\partial^2 g / \partial x_0^2 |_{x_0=x_1} > 0$  (Fig. 3D). This quantity  $\partial^2 g / \partial x_0^2$ , the second derivative of invasion fitness with respect to the trait of the invader, measures the strength of *stabilizing* or *disruptive* selection (Fig. 3C vs. 3D). An ESS represents an endpoint of evolution or community assembly. Note that if new strategies are restricted to be similar to existing ones (*e.g.* due to small mutations), local evolutionary stability is sufficient to prevent further trait change. However, if large mutations or immigration of different species occur, global evolutionary stability is required (Fig. 3C vs. Fig. 3E).

A second form of stability — *convergence stability* — controls whether directional selection leads towards or away from an evolutionary equilibrium (Eshel 1983, Geritz *et al.* 1998). An evolutionary equilibrium is convergence stable when  $\partial^2 g / \partial x_1^2 > \partial^2 g / \partial x_0^2$ . Any combination of these two stability conditions (evolutionary and convergence stability) is possible. An evolutionary equilibrium that is both convergence and evolutionary stable (*i.e.* a fitness maximum) is called a *convergence stable strategy (CSS)*, which behaves as we would naively expect an optimum to behave. While fitness minima play a minor role in optimization models, serving only as boundaries between the basins of attraction of alternative optima (Fig. 2B), they can play a central role in density-dependent models. The most interesting case where the two conditions differ is an evolutionary equilibrium that is convergence stable but not evolutionary stable, which is called a *branching point* (Geritz *et al.* 1998) for reasons discussed below.



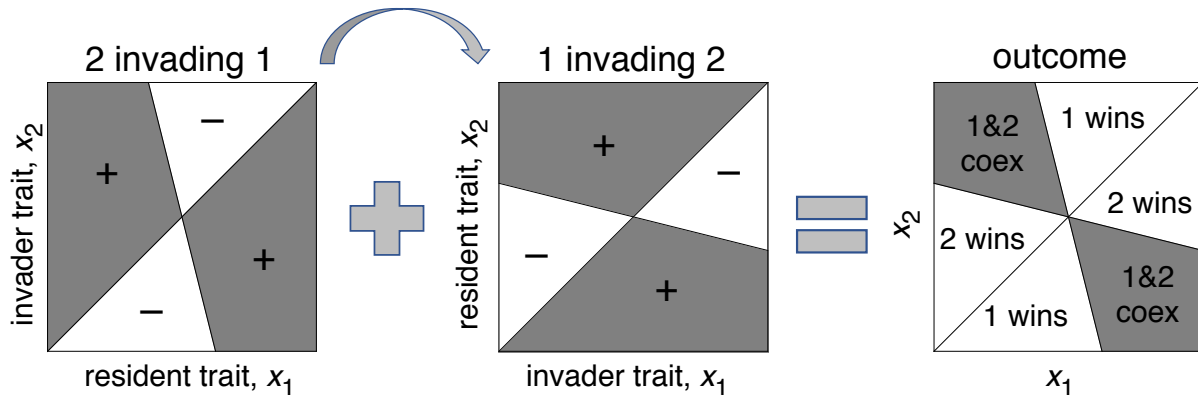
**Figure 3.** Invasion fitness landscapes. Positive invasion fitness is denoted by gray shading. **A-B)** Directional selection. **C)** An evolutionarily stable strategy (fitness maximum). **D)** A branching point (fitness minimum). **E)** A local-but-not-global ESS. **F)** A two-species evolutionarily stable community.

Geritz *et al.* (1998) gives a complete eight-fold classification of the types of stability of monomorphic evolutionary equilibria, both in terms of these second derivatives of invasion fitness and also graphically using *pairwise invasion plots* (PIPs). Whether the invasion of a resident with strategy  $x_1$  by an invader with strategy  $x_0$  is successful or not depends only on the sign of  $g(x_0; \hat{E}(x_1))$  or  $g(x_0; x_1)$  for short. A PIP plots  $\text{sign}[g(x_0; x_1)]$  as a function of the strategy of the resident and the invader (Fig. 4). Graphically, convergence stability can be seen along the main diagonal, whereas evolutionary stability is assessed with a vertical line test through the evolutionary equilibrium.



**Figure 4.** The eight-fold classification of pairwise invasibility plots (PIPs), after Geritz *et al.* (1998). **A, G-H)** Non-convergence stable repellers. **B)** An evolutionary branching point is convergence stable but not evolutionarily stable. **C-E)** Continuous stable strategies (CSSs) are both convergence and evolutionarily stable. **F)** The Garden of Eden is evolutionarily stable but not convergence stable.

A *mutual invasibility plot* (MIP) illustrates the pairs of strategies  $x_1$  and  $x_2$  that can stably coexist, i.e.  $g(x_2; x_1) > 0$  and  $g(x_1; x_2) > 0$ . It is constructed by superimposing a PIP on its reflection around the 1-1 line, exchanging the role of resident and invader (Fig. 5). In general, the region of stable coexistence through mutual invasibility (if one exists) does not touch the 1-1 line, other than at points corresponding to one-strategy evolutionary equilibria. This implies that, in general, similar species cannot coexist, representing an ecological limit to similarity.



**Figure 5.** A mutual invasibility plot (MIP) shows pairs of strategies that can stably coexist. It is made by exchanging the roles of resident and invader by flipping a PIP on itself. After Geritz *et al.* (1998).

One important exception occurs near branching points, where coexistence of similar strategies is guaranteed. This means that a strategy that successfully invades a resident at a branching point does not exclude it, but coexists with it. These coexisting strategies then experience opposing directional selection and diverge, justifying the name “branching point”. The final outcome may be a pair of strategies that prevent invasion (Fig. 3F), or the development of further branching points leading to a more diverse set of strategies, or other outcomes (see section 2.2.6). A set of strategies (or species) that is both globally uninvasive and convergence stable is described as *evolutionarily stable community* (ESC); Fig. 3F illustrates a two-species ESC (Edwards *et al.* 2018; Kremer and Klausmeier 2017). This scenario assumes no recombination between the two diverging lineages, which may not be valid in sexual species (Waxman and Gavrillets 2005). In general, however, the existence of a branching point indicates that more than one ecological strategy is required to render a community uninvasive.

One important caveat about the above discussion of the stability of evolutionary equilibria is that all of the conditions based on derivatives are strictly local criteria. Just as a local optimum may not be a global optimum (Fig. 2B), a local ESS where  $\partial^2 g / \partial x_0^2 < 0$  may be invulnerable by a strategy that is sufficiently different than a resident (Fig. 3E). In this case, assumptions about the source of new phenotypes matters: under the assumption of small mutations (in adaptive dynamics) or standing genetic variation (in quantitative genetics, see section 3), a local-but-not-global ESS would represent a stable equilibrium, whereas larger mutations or immigration of different species from a regional species pool would allow the community to escape such an equilibrium.

### 2.2.5. Trait-based predictions across environmental gradients

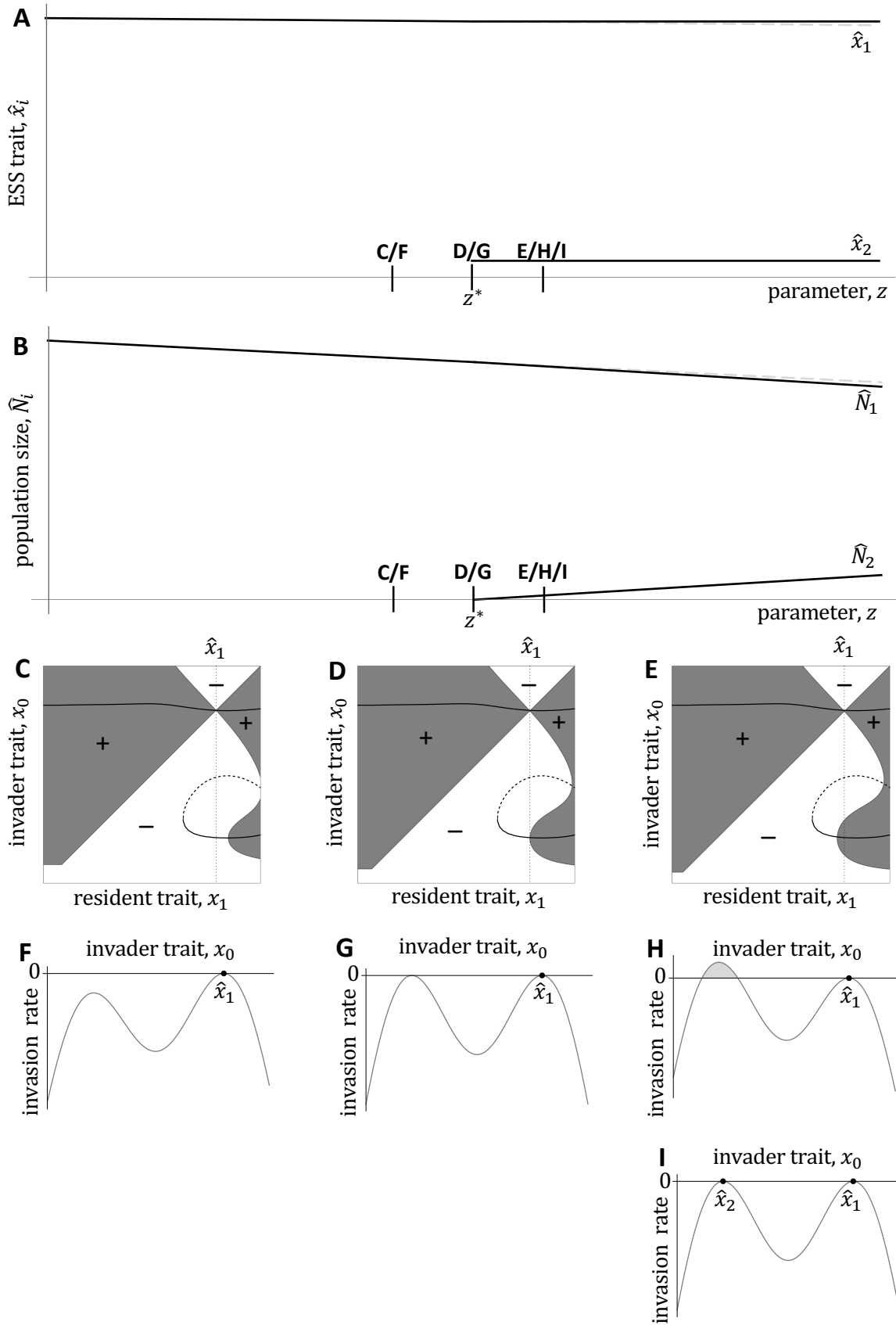
The preceding section offered a detailed description of how to determine the outcome(s) of community assembly/evolution within a community, focusing on particular trait(s), while other model parameters remained fixed. An important application of trait-based approaches is to examine how these outcomes change as these external parameters vary. This can be used to determine how community structure — the diversity and abundance of species present and the value and similarity of their traits — varies with changes in model parameters, including along environmental gradients, a central goal of community ecology.



Other general insights emerge, including revealing how an  $\mathcal{N}$ -species ESC may lose its evolutionary stability as an environmental parameter varies. Intuitively, one might expect that a member of the ESC loses stability as a branching point emerges; however, except when the model has a particular symmetry, the first bifurcation is a loss of global evolutionary stability, resulting in a local-but-not-global ESS (Fig 3E; Geritz *et al.* 1999). At the same parameter value where the ESC first loses its global evolutionary stability an  $(\mathcal{N} + 1)$ -species ESC is created, with the new strategy at zero population density (Fig. 6). Thus, the system is discontinuous in traits but continuous in population density at these *evolutionary transcritical bifurcation* points. Alternatively, an  $\mathcal{N}$ -species ESC may collapse into an  $(\mathcal{N} - 1)$ -species ESC as the density of one of its members declines to zero. This is a developing area of adaptive dynamics/trait-based theory, sometimes described as the ‘bifurcation theory of adaptive dynamics’.

An efficient way to compute bifurcation diagrams of evolutionary equilibria is as follows (Kremer and Klausmeier 2017). At an initial bifurcation parameter value  $z$ , find a (preferably  $\mathcal{N} = 1$  species) ESC by simultaneously solving for the abundance  $\hat{N}_i$  and trait value  $\hat{x}_i$  of each population  $i$  such that  $g(\hat{x}_i; \vec{x}) = 0$  and  $\partial g / \partial x_0(\hat{x}_i; \vec{x}) = 0$ . There are two equations and two unknowns per population, which can be solved numerically using Newton’s method. Then vary the bifurcation parameter value  $z$  by a small amount  $\delta z$  and solve for the updated evolutionary equilibrium, extrapolating the previous solution(s) as an initial guess. At each value of the parameter  $z$ , 1) assess global evolutionary stability by checking that  $\max g(x_0; \vec{x}) < 0$  and 2) verify that no species has gone extinct ( $\hat{N}_i > 0$  for all  $i$ ). These conditions correspond to passing through an evolutionary transcritical bifurcation point either forward (adding a strategy) or in reverse (removing a strategy). Also, 3) check convergence stability using the Jacobian matrix. If the evolutionary equilibrium is still a convergence stable global ESC with no strategy extinct, continue varying  $z$ . Otherwise, stop (refining with a smaller step size  $\delta z$  if necessary). To find the exact bifurcation point, augment the system with the nascent strategy’s eco-evolutionary equations  $g(\hat{x}_{\mathcal{N}+1}) = 0$  and  $\partial g / \partial x_0(\hat{x}_{\mathcal{N}+1}; \vec{x}) = 0$  and two additional unknowns, the trait value of the nascent strategy  $\hat{x}_{\mathcal{N}+1}$  and the parameter value where the bifurcation occurs  $z^*$ . As a new  $(\mathcal{N} + 1)$ -species ESC is created at this point with  $\hat{N}_{\mathcal{N}+1} = 0$ , this solution provides a natural starting point to be continued as above. The resulting evolutionary bifurcation diagrams summarize predictions of how the evolutionarily stable community structure (trait values, diversity, and population densities) varies with changes in a model parameter, such as along an environmental gradient (*e.g.* Kremer and Klausmeier 2017).

**Figure 6. (over)** A bifurcation diagram showing an evolutionary transcritical bifurcation. **A)** Equilibrium traits and **B)** population sizes as a function of an environmental parameter  $z$ . **C-E)** display PIPs occurring **C)** before, **D)** at, and **E)** beyond the bifurcation point  $z^*$ . The solid lines on the PIPs represent local maxima of the fitness landscape and the dashed lines represent local minima. **F-I)** show corresponding fitness landscapes at the **F-H)** one-species and **I)** two-species evolutionary equilibria.



### 2.2.6. More complex possible outcomes

Within a given environment, stable evolutionary equilibria are not the only possible outcome of eco-evolutionary models used to study trait-based theory. In this section we provide a non-exhaustive summary of a growing set of dynamical phenomena that have been discovered and which may provide important insights into various ecological systems.

Limit cycles. Similar to their purely ecological counterparts, eco-evolutionary systems can converge towards limit cycles where species' abundances and traits both fluctuate over time. A classic example of these evolutionary cycles happens in the context of predator-prey co-evolution models (Dieckmann *et al.* 1995, Cortez and Weitz 2014).

Evolutionary suicide. The pessimization principle mentioned earlier illustrates another classic emergent phenomenon of eco-evolutionary models, known more generally as the "Tragedy of the commons" (Hardin 1968). In section 2.2.4 we described how invasion analysis is used to understand the repeated invasion and replacement of resident populations by invaders with different trait values. This sequence of replacements is determined solely by the fitness of new invaders when rare; nothing ensures that a new invader behaves "optimally" when it has completely replaced the former resident. For example, there is no reason in general for the equilibrium population density of successive invaders to increase. In fact, quite the opposite can happen: evolution can drive a population extinct, either through a continuous decrease in density (Dieckmann 2002, Boudsocq *et al.* 2010) or through a catastrophic tipping point in the presence of an Allee-effect at low densities (Ferrière 2000). These phenomena are considered examples of "evolutionary suicide" or "evolutionary traps".

Branching-extinction evolutionary cycles. Another interesting phenomenon happens when one of the two populations generated by a branching point goes extinct through evolutionary suicide (Dercole 2003). If the surviving population remains in the basin of attraction of the original branching point, it will be driven back towards the branching point and diversify, again setting one population up to experience evolutionary suicide. The succession of these branching and extinction events lead to a stable eco-evolutionary limit cycle.

Alternative evolutionarily stable states. Finally, as in purely ecological models, alternative stable states can occur in eco-evolutionary models in the form of alternative ESSs and ESCs (Kisdi and Geritz 1999; Kremer and Klausmeier 2017). Such eco-evolutionary priority effects mean that the initial trait values of evolving population(s) will influence which ESS/ESC is reached at equilibrium. This once again illustrates that "optimality" in density-dependent trait-based models is a subtle concept, as density-independent models generally only possess one global optimum.

### 2.3. Applications

Section 2.2.3 presented a general approach for implementing a trait-based approach using virtually any mechanistic model of community dynamics. It is not surprising then that trait-based approaches have been applied to a broad range of systems in ecology and evolution, to study questions from what determines organism's adaptations to what drives large-scale ecosystem functions. Here we give but a sampling of this extensive literature. Many of the following examples use techniques similar to those described above; others use related methods (see section 3).

This broad spectrum of applications includes a wide range of different types of ecological interactions. In the context of consumer-resource interactions, trait-based models have shown how different resource types influence consumer diversification (Schreiber and Tobiason 2003), as well as revealing optimal allocation strategies for taking up different resources (Abrams 1987) and the effects of resource uptake plasticity (Bonachela *et al.* 2011). When applied to predator-prey interactions, trait-based approaches have shown how evolution can strongly alter predator-prey cycles (Cortez and Weitz 2014) or even engender them (Abrams and Matsuda 1997), and have helped us understand what drives the evolution of prey defenses (Yoshida *et al.* 2003, Koffel *et al.* 2018a). Trait-based models of host-pathogen systems have shown how within-host competition between pathogens is at the origin of their virulence (Van Baalen and Sabelis 1995, Alizon *et al.* 2013) and how spatial structure can lead hosts to evolve altruistic defense strategies, such as suicide upon infection (Débarre *et al.* 2012). A diversity of other trophic situations has been investigated, including mixotrophy (Andersen *et al.* 2015), cannibalism (Dercole and Rinaldi 2002, Hin and de Roos 2019), and intra-guild predation (Patel and Schreiber 2015), the latter two giving rise to a rich set of eco-evolutionary phenomena such as eco-evolutionary cycles and evolutionary suicide. Trait-based approaches have also been applied to positive interactions, *e.g.* to investigate the emergence and maintenance of facilitation in arid ecosystems (Kéfi *et al.* 2008), the role of facilitation in primary succession (Koffel *et al.* 2018b), and the impact of exploiters on the evolution of mutualism (Jones *et al.* 2009).

Trait-based approaches have made it possible to study the evolution of life-history traits in a diversity of organisms and ecological situations, including the size at maturation of exploited fish stocks (de Roos *et al.* 2006), the seed size and germination strategies of terrestrial plants (Geritz *et al.* 1999, Mathias and Kisdi 2002, Levin and Muller-Landau 2000), the foraging behavior of herbivorous arthropods (Egas *et al.* 2005), and the size and trophic strategies of unicellular planktonic organisms (Chakraborty *et al.* 2017).

Trait-based approaches have also been used to understand the emergence of community structure. System-specific models have been applied to shade-tolerant trees competing for light in forests subject to disturbances (Falster *et al.* 2017), phytoplankton-zooplankton systems along nutrient gradients (Sauterey *et al.* 2017), global distributions of phytoplankton (Follows *et al.* 2007), and size-structured fish communities (Hartvig *et al.* 2011). A variety of size-structured food web models have been developed to understand emergent properties such as connectance, omnivory and trophic structure (Loeuille and Loreau 2005, Fuchs and Franks 2010, Banas 2011).

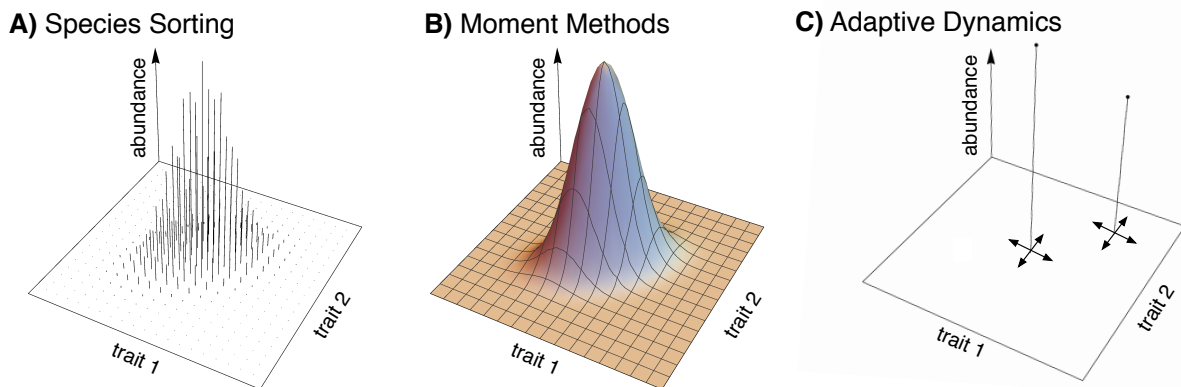
When implemented in ecosystem models with an explicit abiotic environment, trait-based approaches have shed a light on how organismal adaptations affect ecosystem processes. Examples include understanding selection patterns on nitrogen-fixing plants and their consequences for N-limitation in ecosystems (Menge *et al.* 2008, Lu and Hedin 2019), the evolution of plant litter decomposability (Boudsocq *et al.* 2011, Allison 2012, Barot *et al.* 2016, Arnoldi *et al.* 2019), and the determinants of phytoplankton stoichiometry and their effect on oceanic N:P ratios (Lenton and Klausmeier 2007).

### 3. Other Trait-Based Frameworks

As noted in section 2, a plethora of trait-based modeling frameworks have been developed over the years (Abrams 2001, Abrams 2005, Fussmann *et al.* 2007), which we summarize in Table 1. Some of these frameworks are purely ecological, assuming fixed trait values. Others are purely behavioral/evolutionary, neglecting population dynamics. Finally, many combine ecological and evolutionary dynamics in various ways. These frameworks differ in a number of ways:

- the level of biological organization at which traits vary: within individuals (plasticity, including behavior and physiological acclimation), within species (genetic and non-genetic trait variation), or between species
- the heritability of trait variation
- the degree to which biological details are aggregated (do models track population sizes, trait means, and possibly trait variance/covariances, or entire phenotypic distributions?) (Fig. 7)
- the relative timescales of different processes, and
- the source of new phenotypes (mutation or immigration, occasional or continuous)

Despite their differences, these different frameworks are all based on trait-dependent growth functions  $g$  and many can be connected mathematically as limiting cases (Abrams 2001, Lion 2018).

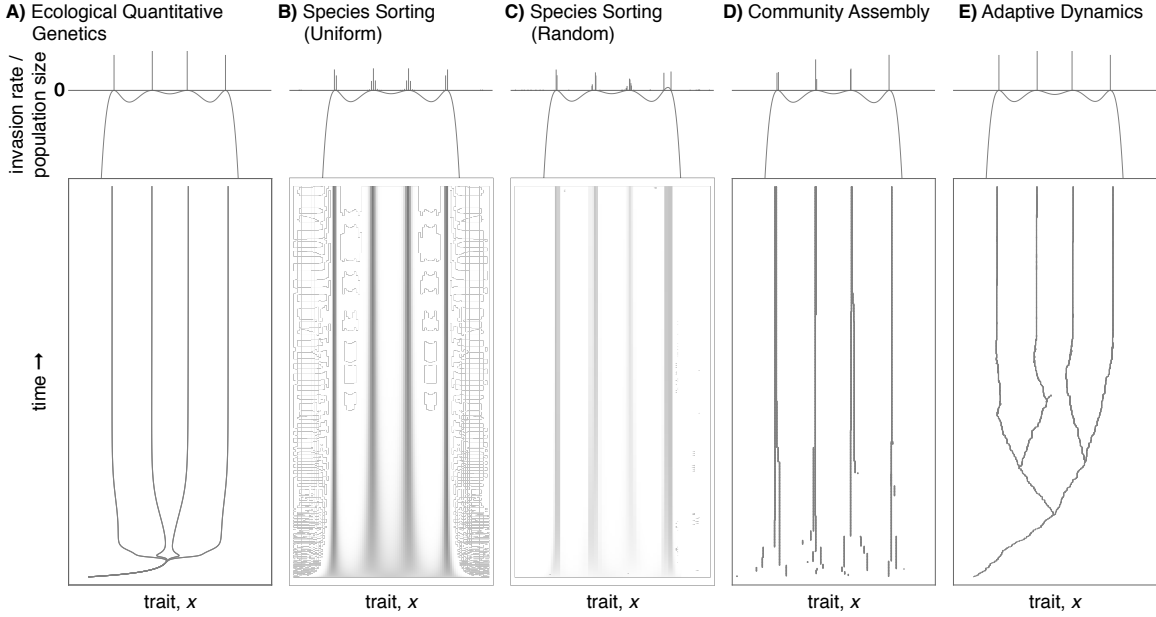


**Figure 7.** Three trait-based modeling frameworks aggregate biological details to different degrees. **A)** Species sorting. **B)** Ecological moment methods. **C)** Adaptive dynamics.

They also can reach similar conclusions about long-term outcome of community assembly / evolution. When there is a global convergence and evolutionarily stable community, these approaches often tend to similar outcomes. For example, Figure 8 shows the outcome of the Lotka-Volterra competition model (Box 1) simulated using five different trait-based theoretical frameworks. The ecological quantitative genetics framework initialized with four similar species leads to the four-species ESC predicted by adaptive statics (Fig. 8A). After a large but finite time, species sorting leads to four distinct clusters of species, which are symmetrical (when initial strategies are regularly spaced, Fig. 8B) and irregular (when strategies are randomly spaced, Fig. 8C). Community assembly (Fig. 8D) and adaptive dynamics (Fig. 8E) also lead to four clusters of

	Modeling Framework	Population Size ( $N$ )	Trait Value ( $x$ )	Trait Variance ( $V$ )	Number of $N \times V$ Sets	Source of New Phenotypes	References
Ecological	Traditional Community Models	dynamic	fixed	zero	one-few	none	Verhulst 1845, Lotka 1920, Volterra 1926
	Species Sorting	dynamic	fixed	zero	many	none	Chase and Leibold 2003, Follows <i>et al.</i> 2007, Bruggeman and Kooijman 2007
	Community Assembly	equilibrated	fixed	zero	dynamic	occasion immigration	Post and Pimm 1983, Rummel and Roughgarden 1985, Law and Morton 1993, Morton and Law 1997
	Moment Methods	dynamic	dynamic	dynamic	one	none or continuous immigration	Wirtz and Eckhardt 1996, Norberg <i>et al.</i> 2001, Savage <i>et al.</i> 2007
	Intraspecific Variability Theory	dynamic	fixed	fixed	one-few	standing phenotypic variation	Hart <i>et al.</i> 2016
Evolutionary	Classical Quantitative Genetics	N/A	dynamic	fixed or variable	one	standing genetic variation or continuous mutation	Lande 1976
	Optimization Theory	N/A	equilibrated	zero	one	plasticity	Stephens and Krebs 1986, Stearns 1992, Roff 2002
Eco-Evolutionary	Trait Diffusion Models	dynamic	fixed	zero	infinite	continuous mutation	Levin and Segel 1985, Lehman and Tilman 1997, Merico <i>et al.</i> 2014
	Ecological Quantitative Genetics	dynamic	dynamic	fixed	few	standing genetic variation	Abrams 2005
	Growth Rate Optimization Theory	dynamic	equilibrated	zero	any	plasticity	Smith <i>et al.</i> 2011
	Adaptive Dynamics	equilibrated	dynamic	zero	dynamic	occasional mutation	Geritz <i>et al.</i> 1998
	Adaptive Statics	equilibrated	equilibrated	zero	dynamic	everything-is-everywhere	Brown and Vincent 1987, Kremer and Klausmeier 2017, Section 2 of this chapter
	Oligomorphic Dynamics	dynamic	dynamic	dynamic	any	continuous mutation	Sasaki and Dieckmann 2011
	Drift Equation	equilibrated	dynamic	dynamic	any	none or continuous mutation	Gorban 2007

**Table 1.** Comparison of trait-based modeling frameworks.



**Figure 8.** The dynamics and long-term outcome of five different modeling frameworks applied to the same trait-based Lotka-Volterra model with a four-species ESC. **A)** Ecological quantitative genetics. **B)** Species sorting, with a uniform distribution of species. **C)** Species sorting, with a random distribution of species. **D)** Community assembly from a continuous species pool. **E)** Adaptive dynamics with small mutations.

species, each containing one or two very similar species, although the transient dynamics vary considerably.

To understand why these distinct frameworks can lead to similar outcomes, consider the oligomorphic dynamics framework (Sasaki and Dieckmann 2011), which tracks the first three moments for a finite number of phenotypic clusters. The “zeroth” moment is the size of population  $i$ ,  $N_i = \int n_i(x)dx$ ; the first moment is its mean trait,  $\bar{x}_i = \int x \cdot n_i(x)dx / N_i$ ; and the second moment is its trait variance,  $V_i = \int (x - \bar{x}_i)^2 n_i(x)dx / N_i$ . In the absence of immigration and mutation, the dynamics of each population are given by

$$\frac{dN_i}{dt} = \int g(x)n_i(x)dx \approx g(\bar{x}_i)N_i + \frac{1}{2}V_i \left. \frac{\partial^2 g(x)}{\partial x^2} \right|_{x=\bar{x}_i} N_i \quad (4a)$$

$$\frac{d\bar{x}_i}{dt} = \frac{1}{N_i} \int x \cdot g(x)n_i(x)dx - \frac{\bar{x}_i}{N_i} \int g(x)n_i(x)dx \approx V_i \left. \frac{\partial g(x)}{\partial x} \right|_{x=\bar{x}_i} \quad (4b)$$

$$\frac{dV_i}{dt} = \frac{1}{N_i} \int (x - \bar{x}_i)^2 g(x)n_i(x)dx - \frac{V_i}{N_i} \int g(x)n_i(x)dx \approx V_i^2 \left. \frac{\partial^2 g(x)}{\partial x^2} \right|_{x=\bar{x}_i} \quad (4c)$$

The moment equations in (4) are closed by assuming a particular phenotypic distribution, usually normal (Norberg et al. 2001). Assuming small trait variance, each extant species at equilibrium is characterized by  $g(\bar{x}_i) = 0$  (from eq. 4a) and  $\frac{\partial g}{\partial x} = 0$  (from eq. 4b) — the same conditions defining an evolutionary equilibrium in adaptive dynamics (see section 2). The condition for convergence stability matches the linear stability of eq. 4b. Finally, eq. 4c shows that trait variance  $V_i \rightarrow 0$  if  $\partial^2 g / \partial x^2 < 0$  — exactly the same condition as for evolutionary

stability (Taylor and Day 1997). Therefore, it is not surprising that these different frameworks give similar results at equilibrium.

When do we expect these other frameworks to give significantly different results from the adaptive statics approach we describe in section 2? We are not aware of precise statements, but here are some suggestions based on intuition and experience:

- In the case of a local-but-not-global ESS (Fig. 3E), the stochastic trait-substitution process of adaptive dynamics will not find a global ESC, whereas a model that allows large mutations or immigration will not get stuck.
- If ecological quantitative genetics or oligomorphic dynamics models are not initialized with a sufficient number of species, they will not find a global ESC. Instead, they will get stuck at a branching point. Furthermore, early trait convergence can reduce the number of distinct species in these simulations, leading to groups of neutral species clustered on a fitness maximum (Edwards *et al.* 2018).
- If there is no global ESC, then the details of how new strategies arise will be important in determining the non-equilibrium dynamics.
- Increasing immigration or mutation rates (in methods that allow this) will increase the trait variance and eventually affect population size (the “demographic load”; e.g. Ronce and Kirkpatrick 2001) and the number and mean traits of phenotypic clusters.

Frameworks with dynamic trait variances such as ecological moment methods and oligomorphic dynamics may fail at branching points, where  $\partial^2 g / \partial x_0^2 > 0$ , because the disruptive selection will cause the trait variance to diverge. Ecological moment methods are especially susceptible to this problem because they attempt to represent an entire community with only three pieces of information: total population size, mean trait, and trait variance. Thus, they are not well-suited to situations where there is a multi-species ESC.

These different frameworks make different simplifying assumptions, so no single approach is best for all purposes. Questions that directly concern the source of new phenotypes obviously require a framework that includes those processes. Trait continuum models make the fewest simplifications, but are the most computationally intensive of the listed approaches, intractably so for more than two traits. Models that aggregate these details in order to follow a small number of variables are required. Ecological moment methods are particularly compact, and each moment embodies a major ecological perspective — total population (ecosystem), mean trait (functional), and trait variance (diversity). However, as described above, they fail at branching points where the variance diverges.

In contrast, the adaptive statics approach presented in Section 2 allows for a dynamic number of species. It makes the simplest assumption about the source of new phenotypes (“everything is everywhere”; Baas Becking 1934, De Wit and Bouvier 2006) and is computationally efficient, making it an elegant approach focused on the ecological mechanisms underlying community structure in the absence of mutation or dispersal limitation. However, as an equilibrium approach, it is unable to deal with trait dynamics on any time scale.

Adaptive dynamics takes a long-term perspective to address the evolutionary origins of diversity. However, given its assumption of asexual reproduction, new phenotypes form populations that are demographically independent of their progenitors. This can seem simplistic from a purely evolutionary biology standpoint, as it neglects the genetic, sexual,



behavioral, and spatial constraints that can prevent reproductive isolation and assortative mating from occurring, and has been the source of ongoing debate (Doebeli *et al.* 2005, Gavrillets 2005).

Questions about short-term adaptive responses to environmental perturbations require a framework with trait variances such as ecological quantitative genetics or oligomorphic dynamics. For such questions, we recommend the ecological quantitative genetics approach, which allows species evolution to occur within a community context (*e.g.* McPeck 2017). Evolution that happens on an ecological time scale can prevent a population whose density is slowly decreasing from going extinct, a phenomenon called “evolutionary rescue” (Gomulkiewicz and Holt 1995). It can also allow persistence in a continuously changing environment if the rate of environmental change is slow enough (Lynch and Lande 1993), although possibly with a tipping point (Osmond and Klausmeier 2018).

Because trait-based approaches can be applied to questions across ecology and evolutionary biology, we need a diverse set of theoretical frameworks. Understanding the relationships among these frameworks (Table 1) as well as their strengths and weaknesses is required to choose the best approach for a given question. Devising new ways to reduce the complexity of ecological communities in our models will remain a valuable pursuit.

#### 4. Extensions/Complications

The trait-based frameworks we have examined so far were discussed in the simple ecological setting of spatial and temporal homogeneity. Real ecosystems are spatially extended and subject to both externally driven and internally generated temporal fluctuations, and this spatial and temporal heterogeneity is known to be an important determinant of population dynamics and community structure. Furthermore, we have focused on the dynamics of single traits, another vast oversimplification. In this section, we discuss how trait-based theoretical frameworks can be made more realistic, and relevant to more systems, by incorporating temporal and spatial heterogeneity and multiple traits.

##### 4.1. Traits in time

The invasion analysis presented in section 2 assumes that a rare, invading population experiences constant conditions (including resident densities and environmental factors). However, these conditions may vary due to externally driven forcing (stochastic or deterministic) or internally generated cycles or chaos. Adaptive dynamics studies of temporally variable systems require calculating an appropriate average invasion rate  $\bar{g}_{\text{inv}}$ , based on the type of variability present within a system and whether there is population structure (Metz *et al.* 1992). Once the value of  $\bar{g}_{\text{inv}}$  has been calculated, all the machinery of adaptive dynamics can be used exactly as presented in section 2: calculating (time-averaged) fitness gradients, locating evolutionary equilibria, and determining their convergence and evolutionary stability.

*Unstructured populations.* In the case of an unstructured population experiencing periodic forcing, we can simply average the instantaneous invasion rate,  $g_{\text{inv}}(x_{\text{inv}}; \vec{E}(t))$ , over a period:

$$\bar{g}_{\text{inv}} = \frac{1}{\tau} \int_0^{\tau} g_{\text{inv}}(x_{\text{inv}}; \vec{E}(t)) dt \quad (5)$$

(Smith and Waltman 1995). It is straightforward to calculate  $\bar{g}_{\text{inv}}$  when cycles arise from external forcing with known period  $\tau$ , but potentially harder when cycles are endogenously generated, as the precise value of  $\tau$  must be determined numerically and may depend on the trait values of resident species. If the environment varies stochastically or chaotically, then the definition of invasion fitness is the limit of eq. (5) as  $t \rightarrow \infty$ . In practice, it is usually not possible to calculate this infinite integral to find the exact invasion rate, so an approximation can be obtained by simply averaging  $g_{\text{inv}}$  over a long interval of time. Note that, because the integral in eq. (5) is linear, the gradient of average fitness needed for adaptive dynamics studies,  $\partial \bar{g}_{\text{inv}} / \partial x_0$ , is equivalent to the average of the gradient of instantaneous fitness

$$\frac{\partial \bar{g}_{\text{inv}}}{\partial x_0} = \frac{1}{\tau} \int_0^\tau \frac{\partial g_{\text{inv}}}{\partial x_0} dt \quad (6)$$

which may be easier to calculate numerically (Kremer and Klausmeier 2017).

*Structured populations.* As described in section 2, in a constant environment invasion fitness is given as the dominant eigenvalue of the transition matrix. Intuition might suggest that, in fluctuating environments, invasion rate could be calculated by simply averaging the dominant eigenvalue of the transition matrix over a period in a periodic system (or over a long interval of time in an aperiodic system). However, that turns out to be incorrect. Instead, obtaining invasion rates requires calculating the dominant Floquet exponent (periodic systems; Klausmeier 2008) or more generally, the dominant Lyapunov exponents (aperiodic systems; Metz *et al.* 1992). In both cases, this must usually be done numerically.

As a final technical note, the definitions of invasion fitness given above are based on the adaptive dynamics framework, and specifically its separation of time scales. When other trait-based modeling frameworks are employed (section 3), other approaches are required. For example, in the ecological quantitative genetics approach, the average trait(s) of a population change in response to instantaneous fitness gradients, which depend in turn on the current environment. As genetic variance approaches zero, trait change slows, and quantitative genetics results converge on those of adaptive dynamics. However, with larger genetic variances, rapid evolution is possible and complex interactions with ecological dynamics may arise (Hairston *et al.* 2005).

Recently we used trait-based models to examine the evolutionary stability of species coexistence in variable environments. We used the adaptive statics framework to investigate two fluctuation-dependent coexistence mechanisms (*sensu* Chesson 2000): relative nonlinearity and the storage effect. We found that relative nonlinearity can easily support an ESC of two species (a fast grower and superior competitor), but higher diversity was improbable (Kremer and Klausmeier 2013). The storage effect is a potentially more powerful coexistence mechanism. When the environment alternates periodically between two states and the period of forcing is large, two species can coexist as an ESC under a wide range of conditions (Miller and Klausmeier 2017). When the environment varies continuously, more species can coexist, with a limit to similarity resulting in species with evenly spaced trait values (Kremer and Klausmeier 2017). We also found more baroque outcomes, such as alternative evolutionary attractors (Miller and Klausmeier 2017, Kremer and Klausmeier 2017). When using the quantitative genetics framework, we found that evolutionarily stable coexistence was robust to a small amount of trait variance, but that larger trait variance allowed rapid evolution leading

to complex dynamics and species convergence, ultimately undermining species coexistence (Kremer and Klausmeier 2013).

#### 4.2 Traits in space

The theoretical framework as described in section 2 implicitly assumes that populations, communities, and ecosystems do not vary in space, or that dispersal between locations is negligible so that spatial patterns can be derived directly from bifurcation diagrams (section 2.2.5). These assumptions simplify the analysis of trait-based theory when they can be empirically justified for particular organisms, scales, or questions (e.g., in well-mixed planktonic systems). However, accounting for space may be essential when: 1) interactions between organisms (and populations) are spatially structured (e.g. competition among terrestrial plants), 2) the trait(s) of interest are directly related to the movement of individuals, or 3) important environmental factors vary in space, such that populations in different locations experience different selective pressures, and dispersal is not negligible. How ecological processes vary in space is the focus of metapopulation, metacommunity, and metaecosystem theories, all of which can be all be integrated with trait-based approaches.

In the adaptive dynamics framework, accounting for space simply consists of adding additional structure to populations. Rather than considering a single, unstructured population, we instead examine a collection of multiple subpopulations (whose dynamics are driven by local processes), that are coupled together by the exchange of individuals through dispersal. When the subpopulations are discrete, well-separated entities, we call them “patches” and their collective population dynamics can be modelled using matrices similar to Leslie matrices

$$\frac{d\vec{N}_i}{dt} = \left( G(x_i; E(\vec{x}, \vec{N})) + D(x_i) \right) \vec{N}_i \quad (7)$$

where  $\vec{N}_i$  is a vector of the abundances of population  $i$  in different patches,  $G$  is a diagonal matrix governing within-patch dynamics and  $D$  is a matrix encoding dispersal among patches. In principle, both local processes and dispersal may depend on trait  $x$ . Alternatively, it is sometimes more appropriate to model populations as continuously distributed through space (Troost *et al.* 2005). In this approach, population dynamics can be modeled using systems of partial differential equations called reaction-diffusion systems, which take the form

$$\frac{\partial N_i}{\partial t} = g(z, x_i; E(\vec{x}(z), \vec{N}(z))) N_i + d(x_i) \frac{\partial^2 N_i}{\partial z^2} \quad (8)$$

where  $z$  denotes the spatial dimension,  $g$  determines the local dynamics, and the last term allows dispersal (Okubo and Levin 2001). Other approaches vary in their level of detail, from explicitly accounting for the discrete nature of individuals to treating entire populations as either present or absent (e.g. patch occupancy models and cellular automata, see Levins 1969, Durrett and Levin 1998, Klausmeier and Tilman 2002).

Whatever the approach, the fitness of an invading strategy is always given by the dominant eigenvalue of the matrix  $(G + D)$  or the linear operator  $g + d \partial^2 / \partial z^2$ , which is its asymptotic population growth rate once a stable spatial structure across all subpopulations is reached (Metz *et al.* 1992, Troost *et al.* 2005, Van Baalen and Rand, 1998). In the case of reaction-diffusion equations, the linear operator usually needs to be approximated by a matrix. The fitness gradient can be calculated numerically using a finite difference approximation or it can be computed directly using techniques from sensitivity analysis (Caswell 2001), providing

additional conceptual insight: under some conditions, the fitness gradient of the population as a whole can be shown to be equal to a weighted average of the local selection gradients, where the weights are the squared abundances of the corresponding subpopulations (Wickman *et al.* 2017).

Moving from the adaptive dynamics framework to the ecological quantitative genetics framework requires a separate equation for trait dynamics (Kirkpatrick and Barton 1997, Case and Taper 2000, Ronce and Kirkpatrick 2001, Norberg *et al.* 2012). In the reaction-diffusion setting, this takes the form

$$\frac{\partial x_i}{\partial t} = V \left. \frac{\partial g}{\partial x_0} \right|_{x_0=x_i} + d \left( \frac{\partial^2 x_i}{\partial z^2} + 2 \frac{\partial \log N_i}{\partial z} \cdot \frac{\partial x_i}{\partial z} \right) \quad (9)$$

where the first term captures local directional selection and the second term incorporates gene flow (the second term of which accounts for asymmetric gene flow due to gradients in population density). This powerful framework allows for the investigation of local adaptation, since the trait values of a population depend explicitly on space  $z$ .

Applications of spatially-explicit trait-based theory span a diverse set of systems, from bacterial biofilms (Nadell *et al.* 2016), to social vertebrates and insects (Lehmann *et al.* 2008), terrestrial plants (Kéfi *et al.* 2018), pathogens (Débarre *et al.* 2012), and plankton in poorly mixed water columns (Troost *et al.* 2005, Wickman *et al.* 2018). It has provided a number of important insights into the evolution of species ranges (Kirkpatrick and Barton 1997, Case and Taper 2000), the response of communities to environmental change (Norberg *et al.* 2012), the maintenance of species diversity in heterogeneous environments (Wickman *et al.* 2018), and the global distributions of plankton (Follows *et al.* 2007).

The evolution of dispersal itself is an extensively studied topic. It has long been recognized that spatial variation alone is not sufficient to favor the evolution of dispersal (Hastings 1983, Dockery *et al.* 1998, Parvinen 1999, Wickman *et al.* 2017). Only the continuous availability of underexploited patches, either at the edge of an invading population, or maintained by regular disturbance or demographic stochasticity, can turn dispersal into an advantageous trait (Ronce 2007). More subtly, dispersal can evolve as an altruistic behavior (*e.g.* when it reduces competition among an organism's kin, despite offering no direct benefits).

More generally, spatially-explicit approaches have been essential to the understanding of the evolution of cooperation and a variety of other altruistic traits (Lion and Van Baalen 2008, Lehmann *et al.* 2008). In completely homogenous systems, altruism is selected against due to the "Tragedy of the commons" (Hardin 1968). Conversely, spatial structure and local dispersal can create "viscous populations" where related individuals tend to cluster in space, favoring the evolution of altruism (Lion and Van Baalen 2008).

#### 4.3 Multiple traits

The theory on evolutionary equilibria and their stability presented in section 2 focused on systems with a single trait. In the real world, an organism can be characterized by a myriad of traits that are all simultaneously under selection. Even though trade-offs can constrain the space of possible trait combinations, any given population's strategy is often determined by its specific values of multiple traits. For this reason, a general trait-based theory that applies to multidimensional traits is necessary.

In practice, setting up a trait-based model with multidimensional traits follows the same recipe laid out in section 2.2.3, except that  $\vec{x}_{G,i}$  is now a vector whose coordinates are the collection of traits defining the  $i^{\text{th}}$  strategy in guild  $G$ . Invasion fitness  $g(\vec{x}_0; \hat{E}(\vec{x}_1))$  of a mutant  $\vec{x}_0$  follows, with the fitness gradient now being a true vector. Evolutionary equilibria are characterized by the trait vectors  $\vec{x}_0$  that cancel out the components of the fitness gradient. Because of fitness interactions between traits — selection on one trait usually depends on other traits — finding a multidimensional evolutionary equilibrium implies solving a system of coupled equations. This also applies if the multiple traits belong to separate guilds, such as co-evolving predator-prey systems, as it comes to no surprise that the optimal trait for a prey will depend on the trait of the predator, and vice-versa. Finally, assessing whether these evolutionary equilibria are evolutionarily stable relies on extending the optimality theory tools presented in section 2.2.4 to multidimensional space, which is done in practice by checking if the Hessian matrix of the invasion fitness is negative definite for unbounded traits. If the trait space is bounded, constrained optimization has to be used instead.

There is another complication, specific to the multi-dimensional nature of this problem, that involves the idea of convergence stability defined in section 2.2.4. This problem has been well-explored in the adaptive dynamics context (Leimar 2009; see also Débarre *et al.* 2014 for a similar approach in ecological quantitative genetics). This complication is subtle, as convergence stability depends on the nature and characteristics of trait variation. In an evolutionary context, genetic variation is usually constrained through correlations — formally encoded in the genetic variance-covariance matrix, also known as the  $G$ -matrix of quantitative genetics (Lande 1979) — such that selection on one trait can lead to evolution of another trait, even when the latter is not under selection. Due to these correlations, convergence stability cannot always be solely assessed using the Jacobian of the fitness gradient (the “selection” part), but can also depend on the exact nature of genetic correlations (the “variation” part). To formalize this issue, Leimar (2009) distinguishes between two notions of convergence stability. The first, “absolute convergence stability”, imposes very restrictive conditions on the Jacobian of the fitness gradient under which an evolutionary equilibrium will be locally convergence stable under any conceivable adaptive path and  $G$ -matrix. The second, “strong convergence stability”, places a weaker condition on the Jacobian under which an evolutionary equilibrium will be locally convergence stable under the most probable evolutionary trajectory. This second definition of convergence stability is weaker than the first one: if an evolutionary equilibrium is only strong convergence stable, one could find some very particular series of mutations allowing escape from this equilibrium (Leimar 2009).

Applications of trait-based theories that involve multiple traits are diverse. Two-dimensional trait spaces, resulting in practice from a three-way trade-off between three traits, are a natural starting point. They have been influential in ecology (Grime 1974) and are associated with counterintuitive outcomes, such as the possibility of positive correlations between two traits when the last one is not controlled for (Van Noordwijk and de Jong 1986). A recent example in plants involves the study of optimal allocation between resource competition and the tolerance of and resistance to herbivory — with the latter two traits corresponding to “defense” (Koffel *et al.* 2018a). We showed that investment in defense is expected to increase along a resource gradient, but that increase in partial resistance, mixed tolerance and resistance, or coexistence of a completely resistant and a tolerant strategy were all possible

outcomes, depending on the shape of the allocation trade-off that constrains the three traits. In another two-dimensional example, Falster *et al.* (2017) showed how a model of plants differing in leaf mass per unit leaf area and height at maturation in a complex forest ecosystem can generate a very diverse community, including a diverse set of shade-tolerant species. In the context of macro evolutionary dynamics, accounting for multiple phenotypic dimensions has been shown to have a strong influence on the structure of the emerging food webs (Allhoff *et al.* 2015). Using a general model of asymmetric competition, Doebeli and Ispolatov (2017) showed that the diversity of strategies that coexist at the end of the diversification process scales exponentially with the number of traits considered.

Despite these applications, most trait-based models focus on a single trait or a pair of traits linked by a hard trade-off (effectively one trait). One barrier to multi-trait models is coming up with a manageable way to define the shape of multi-dimensional trade-offs. A possibility is to base them on a common energetic or material currency, so that total allocation to different traits is constant, while functions with flexible shapes encode whether investment in a specific trait has diminishing or accelerating returns (Koffel *et al.* 2018a). Further investigation of multiple traits — how they affect convergence stability, how to efficiently find eco-evolutionary equilibria, and how to encode multi-dimensional trade-offs — remains an important area for future theoretical development.

## **5. Frontiers of Trait-Based Modeling**

### **5.1 Comparisons with empirical systems**

One of trait-based theory's advantages, as discussed above, is its ability to make quantitative predictions about the diversity and distribution of trait values likely to occur within populations and communities, and how these distributions might change across environmental gradients (sections 2.2.5). In principle, this should provide increased opportunities to test theoretical predictions and models using experimental and observational data. A handful of examples exist, spanning a range of traits, systems, and ecological dynamics. Regarding individual populations and communities in particular environments, examples include studies of the size-dependent flowering strategies of plants (Childs *et al.* 2003; Rees *et al.* 2006; Metcalf *et al.* 2008), the reproductive strategies of female Soay sheep (Childs *et al.* 2011), and the height and distribution of foliage in herbs and trees (Givnish 1982, King 1990). Considering population and community dynamics through time, successful examples include studies of the predatory-prey cycles exhibited in a rotifer/algae system (Yoshida *et al.* 2003), and seasonal patterns in aquatic food webs (Boit *et al.* 2012; Curtsdotter *et al.* 2019). Across environmental gradients, predictions of trait-based theory have been tested by examining variation in forest productivity along elevational gradients (Enquist *et al.* 2017; Fyallas *et al.* 2017), plant allocation to foliage, wood, and fine roots across nitrogen gradients (Dybziński *et al.* 2011), and global relationships between the optimal temperature of phytoplankton species and the mean annual temperatures they experience (Thomas *et al.* 2012). These examples are exciting and highlight the power of trait-based approaches to bridge gaps between the theoretical and empirical world.

However, compared to the extensive (and growing) body of literature focused on theory alone, these empirical tests are few in number. In part, this may reflect challenges posed by the limited availability of high-quality trait data across multiple individuals, species, and

environments over time (e.g. Kremer *et al.* 2016). Excitingly, portions of this constraint are being alleviated through a variety of massive community-wide efforts to compile and publish trait data, especially for terrestrial plants (e.g. TRY database; Kattge *et al.* 2011). We think, however, that it is more likely that the shortage of examples simply reflects the fact that few teams have attempted to bring together trait-based theory with empirical observations. We hope that the introduction to trait-based theory presented in this chapter will help lower the barriers associated with this challenge, while convincing readers of the value of this opportunity to tighten theoretical-empirical linkages and to advance the field of ecology.

## 5.2 Linking trait- and species-based approaches

In this chapter we have focused on purely trait-based approaches, where a species' performance is defined solely by its traits. This is an effective way to reduce model complexity when the number of relevant traits is less than the number of species. However, achieving this reduction requires knowing the identity (and values) of the relevant traits and how best to incorporate them into process-based models, both of which represent significant challenges. When more species are introduced into trait-based models (such as ecological quantitative genetics models) than can persist in an evolutionarily stable community (ESC), distinct species may converge on an adaptive peak to become selectively neutral (terHorst *et al.* 2010, Edwards *et al.* 2018). This may represent a phenomenon that happens in the real world (McPeck 2017, Edwards *et al.* 2018), but it is also potentially symptomatic of situations where trait-based models are missing important functional variation among species. Are there hybrid approaches that would allow us to combine trait-based models with species-based models that account for species-specific differences?

One possibility, inspired by Chesson's modern coexistence theory (Chesson 2000), would be to consider introducing species-specific terms that either affect "fitness differences" or are (de-)stabilizing. To allow for fitness differences, we would simply add a species-specific term  $\epsilon_i$  to a species' growth rate so that

$$\frac{dN_i}{dt} = (g(x_i; E(\vec{x}, \vec{N})) + \epsilon_i)N_i \quad (10)$$

Theoretically, these fitness-difference terms would simply promote dominance by species with higher  $\epsilon_i$  values. The real value of this formulation would be in parameterizing the trait-dependent population dynamics of actual species, where species differences that cannot be attributed to the traits considered would be captured by this species-dependent "error term".

If these species-specific effects are instead (de-)stabilizing, the theoretical implications are more interesting and require more intricate model modifications. For example, these terms could represent species-specific sources of negative density-dependence, such as intraspecific competition for mates or specialized natural enemies (Scheffer *et al.* 2007), or positive density-dependence such as Allee effects (Noest 1997). Negative density-dependence inhibits resident species more than invaders (who are naturally at low density), stabilizing coexistence of slightly inferior and neutral species. In contrast, positive density-dependence inhibits rare invaders compared to established residents, leading to more cases of founder control (section 2, Lotka-Volterra case iv). A systematic exploration of these effects, as well as broader efforts to integrate trait- and species-based approaches, would be valuable.

### 5.3 Using trait-based theory to improve Earth Systems Models

One frontier where trait-based theory is poised to make important contributions involves earth systems modeling. Earth Systems Models (or ESMs) are spatially explicit models of the dynamic physical and chemical interactions of the earth's land, ocean, and atmosphere (Heavens *et al.* 2013). They are used to study the past development of our planet's climate and the operation of global biogeochemical cycles. ESMs are also powerful tools for projecting future environmental and ecological conditions under different anthropogenic climate change scenarios, including shifting species ranges and altered ecosystem function (Heavens *et al.* 2013). While ESMs contain sophisticated descriptions of physical and chemical processes, biological processes (including ecology and evolution) are treated more coarsely, or are absent entirely. Historical factors, critical uncertainties (including the absence of a widely-accepted, general model of ecology), data shortages (needed to parameterize and validate biological sub-models), and computational demands (ESMs are already computationally intensive) all contribute to limit the level of biological detail in ESMs. These constraints are problematic, as ecological and evolutionary processes can significantly affect physical and chemical properties, driving feedbacks that regulate the global carbon cycle. Consequently, making more accurate projections of future environmental conditions from regional to global scales depends in no small part on developing more realistic representations of ecology within ESMs. Fundamentally, this is a question of how to model variation in traits (and hence, ecosystem function) through time and space at a global scale. Trait-based approaches offer promising ways to enhance the flexibility and biological diversity of biogeochemical models (Litchman *et al.* 2015) and ESMs without adding large computational demands.

Currently, the terrestrial and marine components of ESMs typically aggregate earth's vast functional diversity of individuals and species into somewhere between two and a dozen *functional groups* or *functional types*. All members of a single group are assumed to have fixed, identical traits or functions, intended to represent an average individual. Turnover in traits across environments only occurs through changes in the relative abundances of groups, driven by underlying environmental gradients and/or interactions between groups, such as competition or predation. For example, marine systems often contain basic N-P-Z models (where mineral nutrients, N, support a single, generic phytoplankton, P, that is in turn consumed by a generic zooplankton, Z) (*e.g.* Fasham *et al.* 1990). Extensions of this basic structure expand the diversity of plankton functional types considered, based on factors including size (*e.g.* Le Quéré *et al.* 2005; Stock *et al.* 2014). Similarly, terrestrial models, termed Dynamic Global Vegetation Models (DGVMs) tend to focus on the dynamics of a handful of plant functional types representing trees and herbaceous species. Predetermined bioclimatic envelopes control the distribution of each functional group, while environmental (and in some cases, competitive) factors control the relative abundance of each group within a given location (Foley *et al.* 2000; Sitch *et al.* 2003). Critiques of these approaches include: (i) the fact that fixed trait values significantly under-represent the functional variation within and across communities, and (ii) interactions between functional groups are over-simplified have been raised in both terrestrial and marine systems (*e.g.* Van Bodegom *et al.* 2011; Reichstein *et al.* 2014; Litchman *et al.* 2015). Furthermore, there are concerns in terrestrial systems that population demographics and community succession following disturbance are poorly resolved (Fisher *et al.* 2017), and that fixed bioclimatic constraints of functional groups may severely



hamper the ability of DGVMs to predict the effects of climate change, as new, no-analog environments and communities emerge (Van Bodegom *et al.* 2011).

Trait-based approaches offer promising ways to address these shortcomings, in both marine and terrestrial systems. Efforts to build the next generation of more realistic ecosystem models fall into several groups. This includes adding flexibility to functional groups by replacing fixed trait values with trait-environment relationships that are either empirically parameterized (terrestrial, Zaehle and Friend 2010; Van Bodegom *et al.* 2011; Verheijen *et al.* 2015; temperature dependence in marine models, *e.g.* Stock *et al.* 2014) or that emerge from various optimality assumptions (terrestrial, Xu *et al.* 2012; Meir *et al.* 2015; marine, Smith *et al.* 2016). In marine systems, both moment methods (Terseleer *et al.* 2014) and species sorting (Bruggeman and Kooijman 2007; Follows *et al.* 2007; Ward *et al.* 2012) have been investigated. Others have adopted a detailed individual- or agent-based approach, where traits vary across individuals, determining their survival, growth, and reproduction, and hence the transmission of their traits to successive generations (terrestrial, Scheiter *et al.* 2013; Sakschewski *et al.* 2015; marine, Clark *et al.* 2011, 2013). This approach allows for trait variation within communities, as well as emergent patterns of trait variation across environments and adaptation to ongoing environmental change, but comes at substantial computation costs. While the goal of these diverse studies is the eventual development of the next generation of more biologically realistic ESMs, few if any have yet been applied at the full scale of an ESM, but rather focus on regional examples. Sorting out which of these approaches, all variously focused on traits, provides the most useful balance between flexibility, feasibility, and reality at different scales and in diverse systems, awaits further research.

#### 5.4 Final thoughts

As we have seen, trait-based approaches have a long history in ecology and evolution (section 1), extending well before the emergence of trait-based ecology as an identifiable and important paradigm. In recent decades, theoretical frameworks such as adaptive dynamics (section 2) have used evolutionary concepts to provide tools for understanding a diverse set of ecological interactions and systems (section 2.3). An expanding range of trait-based modeling frameworks (section 3), tailored to different situations, may superficially appear quite different, but are in fact they closely related (table 1). Trait-based theory can incorporate complicating factors such as temporal and spatial heterogeneity and multiple traits (section 4). Future developments of trait-based modeling approaches show great promise in advancing both our theoretical and empirical understanding of ecology, from community structure to global ecosystem dynamics (section 5).

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## Glossary of terms

*adaptive dynamics*: a trait-based theoretical framework that allows for the emergence of community structure, assuming infrequent, small mutations of existing strategies

*branching point*: an evolutionary equilibrium that is convergence stable but not evolutionary stable

*competitive exclusion principle*: no more species can coexist at equilibrium than there are shared limiting factors (Levin 1970)

*contemporary niche theory*: a theoretical framework that employs a graphical approach to determine community structure based on zero net growth isoclines (ZNGIs), which summarize the response of organisms to their environment, and impact vectors, which summarize the effect of organisms on their environment (Chase and Leibold 2003)

*convergence stable strategy (CSS)*: an evolutionary equilibrium that is both convergence and evolutionary stable

*convergence stability*: when directional selection pushes a strategy toward an evolutionary equilibrium

*directional selection*: when there is a non-zero fitness gradient

*evolutionary equilibrium*: a trait value or set of trait values where there is no directional selection; also known as a singular strategy

*evolutionarily stable community (ESC)*: an evolutionary equilibrium (usually of >1 species) that is globally evolutionarily stable and convergence stable

*evolutionarily stable strategy (ESS)*: an evolutionary equilibrium that is evolutionary stable, either locally (cannot be invaded by nearby strategies) or globally (cannot be invaded by any other strategy).

*evolutionary transcritical bifurcation*: a bifurcation where an evolutionary equilibrium loses its global evolutionary stability

*fitness*: a synonym for the per capita growth rate,  $g_i$ ; see also *invasion fitness*

*fitness gradient*: the change in fitness with respect to change in a trait value,  $\partial g / \partial x_0 |_{x_0=x_1}$ ; it summarizes the *directional selection* a strategy experiences

*founder control*: an outcome of competition where whichever species reaches equilibrium first excludes the other

*guilds*: groups of species that are functionally similar in a community, which share a fitness function such that species with identical trait values are neutral

*invader*: a population that is rare, attempting to establish among a resident community; grows or declines exponentially

*invasion analysis*: a popular approach to understanding coexistence between two populations, based on whether each population can invade monoculture of the other on its ecological attractor

*invasion fitness*: fitness of a population when it is rare in an environment set by any resident population(s)

*life history theory*: predicts how organisms should optimize their allocation to growth, survival, and reproduction

*limiting similarity*: limits on how similar the trait values of species can be and yet allow them to coexist

*mutual invasibility plot* (MIP): illustrates the pairs of strategies  $x_1$  and  $x_2$  that can stably coexist

*neutral*: populations with identical fitness

*optimal foraging theory*: predicts how organisms should optimize foraging for different resources

*optimization theory*: a framework that assumes that organisms will maximize their fitness, or a fitness proxy

*pairwise invasion plots* (PIPs): used in adaptive dynamics to classify one-species evolutionary equilibria, these plot the sign of  $g(x_0; x_1)$  as a function of the traits of a resident and an invader population

*resident*: a population that is not an invader, i.e., which has reached its ecological attractor

*stabilizing/disruptive selection*: selection that respectively disfavors (or favors) trait values that are more extreme than the focal strategy's, causing trait variance to decrease (or increase)

*stable coexistence*: two populations with a positive invasion fitness

*structured populations*: populations that cannot be described by a single variable, including those with e.g. sex-, age-, stage-, or size-structured

*strategy*: the trait values of a population (or species, in some cases)

*trade-offs*: relationships between non-independent traits that constrain their variation

*trait*: any measurable characteristic of an individual; *functional traits* are those that affect performance and ultimately fitness. See also *strategy*.

*unstructured populations*: populations that can be described by a single variable such as population size or density