A Theoretical Framework for Trait-Based Eco-Evolutionary Dynamics: Population Structure, Intraspecific Variation, and Community Assembly

Jonas Wickman,[1,*] Thomas Koffel,[1,2] and Christopher A. Klausmeier[1,3,4,5]

1. W. K. Kellogg Biological Station, Michigan State University, Hickory Corners, Michigan 49060; and Program in Ecology and Evolutionary Biology, Michigan State University, East Lansing, Michigan 48824; 2. Université de Lyon, Université Lyon 1, CNRS, Laboratoire de Biométrie et Biologie Evolutive UMR5558, Villeurbanne, France; 3. Department of Integrative Biology, Michigan State University, East Lansing, Michigan 48824; 4. Department of Plant Biology, Michigan State University, East Lansing, Michigan 48824; 5. Department of Global Ecology, Carnegie Institution for Science, Stanford, California 94305

Submitted May 17, 2022; Accepted October 18, 2022; Electronically published February 20, 2023

Online enhancements: supplemental PDF.

ABSTRACT: How is trait diversity in a community apportioned between and within coevolving species? Disruptive selection may result in either a few species with large intraspecific trait variation (ITV) or many species with different mean traits but little ITV. Similar questions arise in spatially structured communities: heterogeneous environments could result in either a few species that exhibit local adaptation or many species with different mean traits but little local adaptation. To date, theory has been well-equipped to either include ITV or to dynamically determine the number of coexisting species, but not both. Here, we devise a theoretical framework that combines these facets and apply it to the above questions of how trait variation is apportioned within and between species in unstructured and structured populations, using two simple models of Lotka-Volterra competition. For unstructured communities, we find that as the breadth of the resource spectrum increases, ITV goes from being unimportant to crucial for characterizing the community. For spatially structured communities on two patches, we find no local adaptation, symmetric local adaptation, or asymmetric local adaptation, depending on how much the patches differ. Our framework provides a general approach to incorporate ITV in models of eco-evolutionary community assembly.

Keywords: moment methods, evolutionarily stable communities, adaptive dynamics, quantitative genetics, intraspecific trait variation (ITV).

* Corresponding author; email: jonas.wickman@gmail.com.

ORCIDS: Wickman, https://orcid.org/0000-0002-5695-0027; Koffel, https://orcid.org/0000-0003-1793-8620; Klausmeier, https://orcid.org/0000-0002-6987-5871.

Introduction

In recent years, the need to account for intraspecific variation of functional traits has been increasingly recognized as important for understanding the functioning of ecological communities (Albert et al. 2010; Violle et al. 2012). For example, intraspecific trait variation (ITV) has been shown to be important for detecting niche differentiation and environmental filtering (Paine et al. 2011) and for quantifying how pairwise species interactions affect the total biomass in experimentally assembled communities (Kraft et al. 2014). ITV in functional traits has also been shown to often be substantial compared with variation between species (Siefert et al. 2015).

If species have heritable variation in traits that affect fitness, natural selection will act on that variation, changing the distribution of traits in the community over time. In the long run, a community with a fixed number of species will approach an attractor for the eco-evolutionary dynamics, in the simplest case an equilibrium. However, such an eco-evolutionary equilibrium could still be invasible by other species from outside the community with other trait distributions, and one of the resident species might be under selective forces that result in an "evolutionary branching," where a species ends up at a fitness minimum as a result of directional selection and consequently splits into two (Geritz et al. 1998). Thus, in the longer term, the species richness of a community at an eco-evolutionary equilibrium might not be stable. Eventually, a community that is in equilibrium and is stable to further addition of species may be reached. Such a community has been called an evolutionarily stable community

  https://doi.org/10.1086/723406

(ESC); since such a community can persist over long timescales and serves as an attractor for eco-evolutionary dynamics, ESCs can serve as important model communities (Edwards et al. 2018).

If both the number of species and the trait variation within each species are driven by eco-evolutionary dynamics, this then raises questions regarding how trait variation is apportioned between and within species in ESCs. For example, what happens when selection goes from stabilizing to disruptive? In general, this can depend on many factors—including genetic architecture, phenotypic plasticity, and mating patterns (Rueffler et al. 2006)—but even in simplified, purely phenotypic trait-based modeling, theory gives different answers depending on the basic assumptions the theory uses. When the theory includes ITV but fixes the number of species, weaker stabilizing selection will lead to more ITV (Kimura 1965; Bürger 1986), whereas in theory where the number of species is dynamic but with no ITV, weaker stabilizing selection will lead to more species coexisting (Levins 1962; MacArthur and Levins 1964; Dieckmann and Doebeli 1999). If one could incorporate both facets, the actual ESC would likely be some combination of the two, but whether the ESC will comprise a few species with great ITV or many species with little ITV cannot currently be determined, as theoretical approaches for assembling ESCs that take ITV into account are not yet developed.

This tension between ITV and species coexistence can also play out in spatially structured communities. Given sufficient heritable trait variation, spatially varying selection can lead species' traits to vary across space, resulting in different degrees of local adaptation (Kirkpatrick and Barton 1997; Bruggeman 2009; Norberg et al. 2012; Le Gland et al. 2020). However, when all individuals of a species are assumed to be identical, local adaptation is not possible, but variable spatial conditions can promote species coexistence (Troost et al. 2005; Débarre and Gandon 2010; Fortelius et al. 2015; Wickman et al. 2017, 2019). Thus, to cover trait space on the regional scale, an ESC might comprise a few species with substantial local adaptation or many species with little local adaptation.

The current state of eco-evolutionary theory is not well equipped to deal with these questions. On one hand, quantitative genetics (Lande 1979; Lande and Arnold 1983) and other moment equation–based frameworks (Wirtz and Eckhardt 1996; Norberg et al. 2001; Savage et al. 2007; Sasaki and Dieckmann 2011; Merico et al. 2014) readily incorporate ITV into the models. However, even the versions of these models that can treat multiple species (Sasaki and Dieckmann 2011; Débarre et al. 2014) assume that the number of species is fixed rather than a dynamic outcome of eco-evolutionary community assembly. On the other hand, using a different modeling approach called adaptive dynamics (Metz et al. 1992; Dieckmann and Law 1996; Geritz et al. 1998; Dercole and Rinaldi 2008; Brännström et al. 2013) one can easily determine whether a community is closed to evolutionary branching and/or invasion by other species. Thus, using adaptive dynamics, one can assemble a community that is not only at an eco-evolutionary equilibrium but that is also stable against further diversification into more species by invasion or evolutionary branching. However, by construction, adaptive dynamics assumes that all individuals within a species are identical, so it cannot take ITV into account. While model-specific studies in structured communities that combine species assembly with ITV have been carried out (Débarre et al. 2013) and the moment equations for a fixed number of species for a general category of class-structured communities has recently been developed (Lion et al. 2022), a framework for systematically assembling ESCs that take ITV into account does not exist.

In this article we synthesize many recent advances in describing eco-evolutionary dynamics through moment equations taking the total density, mean traits, and trait variances into account and adapt the community assembly capabilities of adaptive dynamics to work with these moment equations. This yields a general framework for eco-evolutionary community assembly for class-structured communities that allows us to assemble ESCs that include ITV. The framework can handle complex models that include multiple traits and external resources, but in the main text we will focus on resolving the twin tensions described above regarding whether trait diversity will be apportioned within or between species as well as within a local community or across a spatial gradient. We illustrate the framework using two simple models of Lotka-Volterra competition. First, we describe the framework in the simplest possible setting without population structure and use the first Lotka-Volterra model to investigate the simultaneous increase in ITV and number of species that results from weaker stabilizing selection. We then extend the framework to class-structured populations, which we illustrate with a two-patch spatially structured Lotka-Volterra model to investigate the tension between local adaptation and species coexistence as the two patches become increasingly different. These analyses show that rich patterns of intra- and interspecific trait variation emerge even in these simple models and thus demonstrate the utility we believe this framework has for furthering our understanding of the interaction between eco-evolutionary dynamics and individual variation in traits.

Eco-Evolutionary Dynamics and Community Assembly in Unstructured Communities

In this section we will introduce the trait space equations that underlie our approach and describe how these

equations can be approximated by moment equations that track the total densities, mean traits, and trait variances of several species. We will then explain how these equations can be used in conjunction with a community assembly approach to determine the ESC. To explore the tension between ITV and species coexistence, we employ a simple Lotka-Volterra competition model.

Trait Space Equations for Unstructured Communities

We consider a single trait value x that encodes some property of an organism, such as body mass or resource-uptake ability. The entire community can then be described by the trait density distribution $v(x)$, which tells us how many individuals there are with trait x; to be more precise, $\int_a^b v(x)\mathrm{d}x$ describes the total density of individuals that have a trait value in the interval $a \le x \le b$. We assume that the density of individuals grows as a result of births with per capita rate $b(x, v)$ and declines as a result of mortality with per capita rate $m(x, v)$, where both birth and death rates can depend both on the trait of an individual, x, and on the entire trait density distribution in which the individual exists, v. We will assume that reproduction is clonal but that parents do not give birth to exact copies of themselves but instead produce offspring with normally distributed traits. Thus, a parent with trait y will produce offspring with trait x according to

$$\mathcal{N}(x, y, M) \coloneqq \frac{1}{\sqrt{2\pi M}} \exp\left(-\frac{(x-y)^2}{2M}\right), \tag{1}$$

where M is the mutation variance. We will use the notation $\mathcal{N}(x, \mu, V)$ throughout for the probability-density function of a normal distribution with mean μ and variance V evaluated at x. As in adaptive dynamics and trait diffusion approaches (Merico et al. 2014; Le Gland et al. 2020; Nordbotten et al. 2020), we do not specify the genetic makeup that would result in these dynamics for phenotypic traits but simply assume that new heritable variation is generated through mutations that are associated with some ecological process, such as births.

We can now write how the trait density distribution will change over time, which is given by the equation

$$\frac{\mathrm{d}v(x)}{\mathrm{d}t} = \int_{-\infty}^{\infty} b(y, v)v(y)\mathcal{N}(x, y, M)\mathrm{d}y - m(x, v)v(x), \tag{2}$$

where $\mathcal{N}(x, y, M)$ is the normal mutation kernel with variance M, describing how different offspring are from their parents on average. We will refer to these types of equations as "trait space equations." These models are similar to classic work in quantitative genetics (Kimura 1965; Bürger 1986), and models like this have been shown to be the limit of certain individual-based models in the limit of large populations (Champagnat et al. 2006).

Trait Space Equations for the Unstructured Lotka-Volterra Model. To take a concrete example, we will consider a simple model of Lotka-Volterra competition (Lotka 1925; Volterra 1928). The model is similar to Lotka-Volterra models in many other recent studies using, for example, oligomorphic dynamics (Sasaki and Dieckmann 2011), quantitative genetics (Barabás et al. 2022), and adaptive dynamics (Ranjan and Klausmeier 2022). For this model, we assume that individuals experience an environmentally determined intrinsic growth rate $r(x)$ in the absence of other individuals, which is due to a spectrum of resources the individuals exploit. We split the intrinsic growth rate into a birth rate $b(x)$ and background death rate $\mu(x)$. Additionally, all individuals experience extra density-dependent mortality due to competition with all other individuals, at a per capita rate $a(x, v)$, in a way such that competition is most intense between individuals with similar traits. Comparing with equation (2), we thus have that $m(x, v) = \mu(x) + a(x, v)$, and the trait space equations are given by

$$\frac{\mathrm{d}v(x)}{\mathrm{d}t} = \int_{-\infty}^{\infty} b(y)v(y)\mathcal{N}(y, x, M)\mathrm{d}y - \mu(x)v(x) - a(x, v)v(x), \tag{3a}$$

$$b(x) = r_0, \quad \mu(x) = \frac{x^2}{V_\mathrm{r}}, \quad r(x) = b(x) - \mu(x) = r_0 - \frac{x^2}{V_\mathrm{r}}, \tag{3b}$$

$$a(x, v) = \int_{-\infty}^{\infty} \alpha(y, x)v(y)\mathrm{d}y, \quad \alpha(y, x) = \exp\left(-\frac{(y-x)^2}{2V_\mathrm{c}}\right). \tag{3c}$$

Here, V_r is the resource spectrum variance and V_c is the competition variance, which is a measure of how broad competition is in trait space, with larger V_c increasing competition between individuals of different traits. For $V_\mathrm{c} \to 0$ individuals will compete only with other individuals with exactly the same trait, and for $V_\mathrm{c} \to \infty$ individuals will compete equally with individuals with any trait. Trait-matching competition of this type can be motivated, for example, by the fact that birds with similarly sized beaks will compete more strongly since they compete for similarly sized seeds (MacArthur 1972).

In general, the generic trait space equations (eq. [2]) will not be analytically tractable; even the equilibrium of equation (2) will be hard to ascertain, even for very simple examples (e.g., Kimura 1965; Bürger 1986). Numerically too, discretizing trait space and solving equation (2) often requires significant computational power. For the more complicated

models we will study later in this article especially, the feasibility of numerical explorations of the equations is highly limited. Instead, we will study approximations of the trait space equations where the moments of the trait density distribution are tracked. Such moment equations have the additional benefit that they are often more ecologically interpretable than the trait space equations.

Moment Equations for Unstructured Communities

Here, we will follow the general approach of previous moment-based frameworks (Slatkin 1980; Wirtz and Eckhardt 1996; Norberg et al. 2001; Bruggeman 2009; Sasaki and Dieckmann 2011; Tirok et al. 2011; Merico et al. 2014; Débarre et al. 2014; Nordbotten et al. 2020) to derive approximate equations that track the total density, mean trait, and trait variance of populations. These approaches, and ours, all result in similar equations, but as the details differ we will here detail the precise assumptions we make to derive these equations. We will assume that the trait density distribution $v(x)$ can be decomposed into a set of S "species," where each species represents a peak in the trait density distribution so that

$$v(x) = \sum_{i=1}^{S} v_i(x). \tag{4}$$

We will then assume that each such species can be approximated with a normal distribution so that

$$v_i(x) \approx u_i \mathcal{N}(x, \bar{x}_i, V_i), \tag{5}$$

where $u_i = \int_{-\infty}^{\infty} v_i(x)\mathrm{d}x$ is the total density of species i, $\bar{x}_i = (1/u_i)\int_{-\infty}^{\infty} x v_i(x)\mathrm{d}x$ is the mean trait of species i, and $V_i = (1/u_i)\int_{-\infty}^{\infty}(x - \bar{x}_i)^2 v_i(x)\mathrm{d}x$ is the trait variance of species i. We will use the notation

$$\tilde{v}(x) := \sum_{i=1}^{S} u_i \mathcal{N}(x, \bar{x}_i, V_i) \approx v(x) \tag{6}$$

for the approximate trait density distribution. In words, the approximate community trait density distribution $\tilde{v}(x)$ is the sum of all normal trait density distributions for each species, $u_i\mathcal{N}(x, \bar{x}_i, V_i)$. We will assume that each species is reproductively isolated so that individuals born in species i end up as species i individuals. Finally, for the birth rate $b(x, v)$ and mortality rate $m(x, v)$ we will introduce notation that describes the population-level per capita rates for a normally distributed population with mean trait $\bar{x}$ and trait variance V in the environment set by the resident community with trait density $\tilde{v}$. These population-level rates are given by the Gaussian integrals

$$\hat{b}(\bar{x}, V, \tilde{v}) := \int_{-\infty}^{\infty} b(x, \tilde{v})\mathcal{N}(x, \bar{x}, V)\mathrm{d}x, \tag{7a}$$

$$\hat{m}(\bar{x}, V, \tilde{v}) := \int_{-\infty}^{\infty} m(x, \tilde{v})\mathcal{N}(x, \bar{x}, V)\mathrm{d}x. \tag{7b}$$

Given these assumptions, without further approximation we can derive the following equations for the total densities, mean traits, and trait variances for each species $i = 1, \ldots, S$ (for the derivation, see sec. S1 of the supplemental PDF):

$$\frac{\mathrm{d}u_i}{\mathrm{d}t} = \Big(\underbrace{\hat{b}(\bar{x}_i, V_i, \tilde{v}) - \hat{m}(\bar{x}_i, V_i, \tilde{v})}_{\substack{\text{population-level per capita} \\ \text{net growth}}} \Big)\, u_i, \tag{8a}$$

$$\frac{\mathrm{d}\bar{x}_i}{\mathrm{d}t} = V_i \Bigg(\underbrace{\frac{\partial \hat{b}}{\partial \bar{x}}(\bar{x}_i, V_i, \tilde{v}) - \frac{\partial \hat{m}}{\partial \bar{x}}(\bar{x}_i, V_i, \tilde{v})}_{\text{directional selection}} \Bigg), \tag{8b}$$

$$\frac{\mathrm{d}V_i}{\mathrm{d}t} = V_i^2 \Bigg(\underbrace{\frac{\partial^2 \hat{b}}{\partial \bar{x}^2}(\bar{x}_i, V_i, \tilde{v}) - \frac{\partial^2 \hat{m}}{\partial \bar{x}^2}(\bar{x}_i, V_i, \tilde{v})}_{\text{stabilizing/disruptive selection}} \Bigg) + \underbrace{\hat{b}(\bar{x}_i, V_i, \tilde{v})M}_{\text{mutation}}. \tag{8c}$$

We will refer to these equations as "moment equations." Equation (8a) describes how the total density u_i of species i increases in response to its population-level birth rate $\hat{b}(\bar{x}, V, \tilde{v})$ evaluated at its mean trait $\bar{x}_i$ and trait variance V_i and how it decreases in response to the population-level mortality rate $\hat{m}(\bar{x}, V, \tilde{v})$. Note that the birth and mortality rates may depend on the approximate trait density distribution $\tilde{v}$ of the entire community, not just conspecifics. Equation (8b) describes how the mean trait $\bar{x}_i$ of species i responds to directional selection. The mean trait will move along the selection gradient induced by births and deaths toward mean traits that yield higher per capita net growth, similar to the gradient dynamics of the canonical equation of adaptive dynamics (Dieckmann and Law 1996; Champagnat 2003) or in quantitative genetics (Lande and Arnold 1983). The speed at which this directional selection acts depends on the selection gradient multiplied by the level of trait variance V_i in species i, but note that here the selection gradients themselves, $\partial\hat{b}/\partial\bar{x}$ and $\partial\hat{m}/\partial\bar{x}$, can also depend on the trait variance (due to eqq. [7]). Equation (8c) describes how the trait variance V_i of species i responds to stabilizing/disruptive selection and mutations. Selection is stabilizing—resulting in a reduction in trait variance over time—if the sign of the sum of the second derivatives is negative, and selection is disruptive—resulting in an increase in trait variance over time—if the sign is positive. The second term corresponds to an increase in trait variance over time due to mutations, which depends on the population-level per capita birth rate $\hat{b}$ as well as the mutation kernel variance M.

Moment Equations for the Unstructured Lotka-Volterra Model. To get the moment equations for our Lotka-Volterra model, we first need to compute the population-level rates, which can be calculated to be (see sec. S3 of the supplemental PDF)

$$\hat{b}(\bar{x}, V) = r_0, \tag{9a}$$

$$\hat{r}(\bar{x}, V) = \hat{b}(\bar{x}, V) - \hat{\mu}(\bar{x}, V) = r_0 - \frac{\bar{x}^2 + V}{V_r}, \tag{9b}$$

$$\hat{a}(\bar{x}, V, \tilde{v}) = \sqrt{2\pi V_c} \sum_{j=1}^{S} u_j \mathcal{N}(\bar{x}, \bar{x}_j, V + V_j + V_c). \tag{9c}$$

Having done this, we can plug these expressions into the general moment equations (eqq. [8]), which yields the equations

$$\frac{\mathrm{d}u_i}{\mathrm{d}t} = \Bigg[\underbrace{\left(r_0 - \frac{\bar{x}_i^2 + V_i}{V_r} \right)}_{\substack{\hat{r}(\bar{x}_i, V_i) = \\ \hat{b}(\bar{x}_i, V_i) - \hat{\mu}(\bar{x}_i, V_i)}} - \underbrace{\sqrt{2\pi V_c} \sum_{j=1}^{S} u_j \mathcal{N}_{ij}}_{\hat{a}(\bar{x}_i, V_i, \tilde{v})} \Bigg] u_i, \tag{10a}$$

$$\frac{\mathrm{d}\bar{x}_i}{\mathrm{d}t} = V_i \Bigg[\underbrace{-\frac{2\bar{x}_i}{V_r}}_{\frac{\partial \hat{r}}{\partial \bar{x}}(\bar{x}_i, V_i)} + \underbrace{\sqrt{2\pi V_c} \sum_{j=1}^{S} u_j \frac{\bar{x}_i - \bar{x}_j}{V_i + V_j + V_c} \mathcal{N}_{ij}}_{-\frac{\partial \hat{a}}{\partial \bar{x}}(\bar{x}_i, V_i, \tilde{v})} \Bigg], \tag{10b}$$

$$\frac{\mathrm{d}V_i}{\mathrm{d}t} = V_i^2 \Bigg[\underbrace{-\frac{2}{V_r}}_{\frac{\partial^2 \hat{r}}{\partial \bar{x}^2}(\bar{x}_i, V_i)} + \underbrace{\sqrt{2\pi V_c} \sum_{j=1}^{S} u_j \frac{V_i + V_j + V_c - (\bar{x}_i - \bar{x}_j)^2}{(V_i + V_j + V_c)^2} \mathcal{N}_{ij}}_{-\frac{\partial^2 \hat{a}}{\partial \bar{x}^2}(\bar{x}_i, V_i, \tilde{v})} \Bigg] + \underbrace{r_0}_{\hat{b}(\bar{x}_i, V_i)} M, \tag{10c}$$

where $\mathcal{N}_{ij} = \mathcal{N}(\bar{x}_i, \bar{x}_j, V_i + V_j + V_c)$. The growth rate of the total density u_i of species i (eq. [10a]) depends on the environmentally determined intrinsic growth rate, which is determined by the species' distance in trait mean $\bar{x}_i$ from the optimal trait $\bar{x}_i = 0$ and decreased due to the species' trait variance V_i. The species then suffers additional mortality from intra- and interspecific competition, which depends on the mean traits and trait variances of both the focal species i and its competitor j. Interspecific competition is most intense between species whose mean traits $\bar{x}_i$ and $\bar{x}_j$ are close and is mediated by the trait variance of both species i and j as well as the competition variance V_c.

The rate of change of the mean trait $\bar{x}_i$ of species i (eq. [10b]) depends on the directional selection induced by both the intrinsic growth rate and competition. The first term, which is the selection induced by the resource spectrum, always exerts selective pressure toward the optimal trait $\bar{x}_i = 0$. The second term, which is the selection induced by competition, always exerts selective pressure for the mean traits of any species to separate from one another.

The rate of change of the trait variance V_i of species i (eq. [10c]) depends on stabilizing/disruptive selection induced by the resource spectrum and competition. The first term, due to the resource spectrum, is always stabilizing and acts to reduce trait variance over time. This is because the quadratic intrinsic growth rate universally disfavors trait variance. The second term, due to competition is stabilizing if $(\bar{x}_i - \bar{x}_j)^2 > V_i + V_j + V_c$ and disruptive if the opposite is true. For intraspecific competition ($i = j$) the difference between the means is zero, so intraspecific competition is always disruptive. This is because a species with more trait variance will have its individuals more spread out in trait space and consequently suffer less intraspecific competition. If two different species are far enough apart, selection will act stabilizingly on both species to reduce their overlap in trait space by reducing the trait variance of both species. The final term is the mutation term, which always acts to increase trait variance over time.

Together, equations [10] describe the dynamics of the first three moments (zeroth: total density; first: mean trait; second: trait variance) of each species in a community of S species. As we have made a normal approximation for the trait density distribution for each species, no higher moments have to be tracked. We further discuss our choice of normal approximation in the discussion section.

Eco-Evolutionary Community Assembly for Unstructured Communities

So far we have derived how to treat a fixed number of species, S, and their eco-evolutionary dynamics, including the effects on the intraspecific trait variance of the species, but this then raises the question: how many species can coexist? For our Lotka-Volterra model (eqq. [10]) we can see an example of how there exists an intrinsic tension between large intraspecific variance and the number of species: intraspecific competition will increase trait variance and interspecific competition can reduce it; thus, under weak stabilizing selection (e.g., small V_c or large V_r) will we get many species with small trait variance or a few—or even just one—species with large trait variance? Likely the answer is some combination of the two, but without some method for being able to ascertain whether a community where intraspecific variation is taken into account is open to the addition of more species, it is not possible to determine the relative importance of these two effects.

To be able to answer these questions, we need to adapt the eco-evolutionary community assembly methods available in adaptive dynamics. Specifically, we devise a method for determining whether a species in a community can undergo evolutionary branching when in equilibrium and a method for determining whether a community is invasible by any other rare species.

Evolutionary Branchings. In adaptive dynamics, evolutionary branching occurs when a species has evolved a trait in accordance with directional selection until directional selection ceases and the species finds itself at a fitness minimum causing the species to split in two (Geritz et al. 1998). This procedure cannot be directly translated to our moment equation framework due to the fact that we include trait variance. Instead, after equations (8) have reached an equilibrium for S species we virtually split each species into two identical copies and examine the linear stability of the resulting $S + 1$ species equilibrium. If such a split-species equilibrium is unstable, we say that the system has undergone an evolutionary branching and keep the split-species pair. The details of the procedure are available in section S2 of the supplemental PDF. Figure 1 depicts an example of a branching in the Lotka-Volterra model.

Invasion Analysis. Even if no evolutionary branchings are possible, the community might not be closed to invasion by types that are farther away in trait space. We will here employ a scheme for carrying out a global invasion analysis inspired by Kremer and Klausmeier (2013). To determine whether a community is closed to invasion, we introduce a rare invading population with mean trait $\bar{x}^{\text{inv}}$ and trait variance V^{inv} into a resident community whose species are all in equilibrium. Let $\tilde{\nu}^{\text{res}}$ denote the sum-of-normals trait density distribution of the residents. As we assume that the invader will initially remain rare, we do not need to track its total density, and the equations for its mean trait and trait variance are given by

$$\frac{\mathrm{d}\bar{x}^{\text{inv}}}{\mathrm{d}t} = V^{\text{inv}}\left(\frac{\partial \hat{b}}{\partial \bar{x}}(\bar{x}^{\text{inv}}, V^{\text{inv}}, \tilde{\nu}^{\text{res}}) - \frac{\partial \hat{m}}{\partial \bar{x}}(\bar{x}^{\text{inv}}, V^{\text{inv}}, \tilde{\nu}^{\text{res}})\right), \tag{11a}$$

$$\frac{\mathrm{d}V^{\text{inv}}}{\mathrm{d}t} = (V^{\text{inv}})^2\left(\frac{\partial^2 \hat{b}}{\partial \bar{x}^2}(\bar{x}^{\text{inv}}, V^{\text{inv}}, \tilde{\nu}^{\text{res}}) - \frac{\partial^2 \hat{m}}{\partial \bar{x}^2}(\bar{x}^{\text{inv}}, V^{\text{inv}}, \tilde{\nu}^{\text{res}})\right) + \hat{b}(\bar{x}^{\text{inv}}, V^{\text{inv}}, \tilde{\nu}^{\text{res}})M, \tag{11b}$$

where we note that the invader rates depend only on the resident densities, because we assume it to be so rare that its effect on itself is negligible.

As long as the invader starts out sufficiently rare, we can assume that its mean trait and trait variance will settle onto an attractor, in the simplest case an equilibrium, where its exponential growth rate can be determined (see Lin et al. 2020). Since the invader moment equations are nonlinear, several attractors may possibly exist. We will here assume equilibrium dynamics, and we can thus assume that a rare

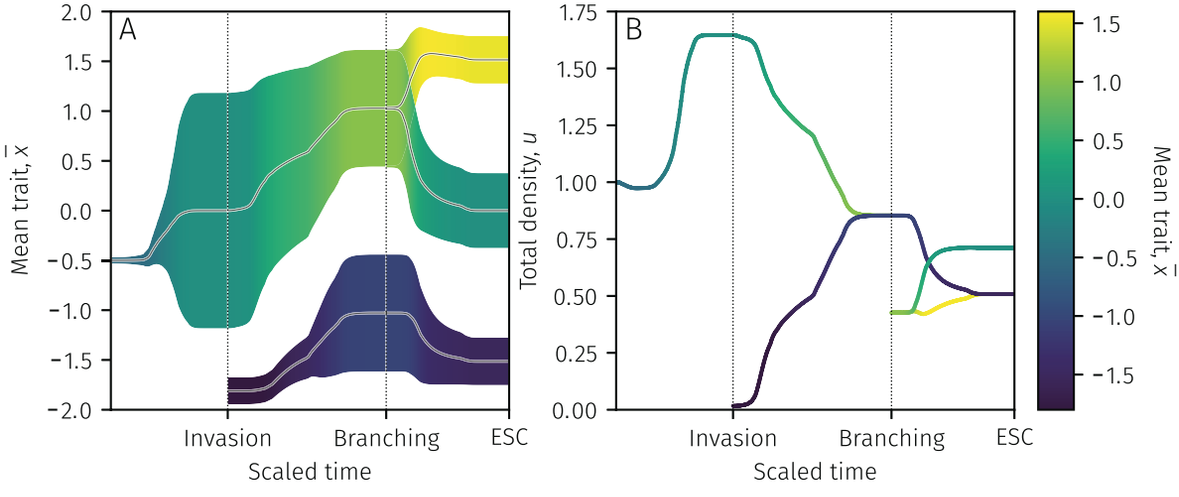

Figure 1: Community assembly through invasion and branching in the unstructured Lotka-Volterra model. The panels depict how mean traits $\bar{x}_i$ and trait variances V_i (*A*; 1 standard deviation is depicted as a filled area) and the total densities u_i (*B*) evolve over time during a community assembly procedure. To start with, a single species with initial moments $u = 1, \bar{x} = -0.5$, and $V = 0.001$ is introduced. Selection from the resource spectrum and competition leads to changes in the density, mean trait (ecological character displacement; Slatkin 1980), and variance according to equations (10), until it reaches an eco-evolutionary equilibrium (first dotted line). Then the system is checked for whether any branchings or invasions are possible. In this case, no branching is possible, but an invader with positive invasion fitness is found and introduced. After that, equations (10) are once again run for the two-species community until it reaches an eco-evolutionary equilibrium (second dotted line). Here, a branching is detected and the top species is split into two new species with slightly different mean traits. We then once again solve equations (10) until equilibrium, during which the branching species diverge. At the final time point the system is once again at an eco-evolutionary equilibrium and no branchings or invasions are possible, meaning that we have reached a three-species eco-evolutionarily stable community. To show all pertinent events, time has been rescaled nonuniformly. Parameter values: $V_{\text{r}} = 9.0$, $M = 10^{-4}$, and other parameters are as in table 2. ESC = evolutionarily stable community.

invader will eventually settle onto one of several equilibria. Assume that there are N such equilibria and denote invaders' means and variances by $\bar{x}^{\mathrm{inv},n}$ and $V^{\mathrm{inv},n}$, respectively, for equilibrium $n = 1, \ldots, N$. Once an invader's trait distribution has reached an equilibrium mean and variance, we can calculate its per capita growth λ_n as

$$\lambda_n = \hat{b}(\bar{x}^{\mathrm{inv},n}, V^{\mathrm{inv},n}, \bar{v}^{\mathrm{res}}) - \hat{m}(\bar{x}^{\mathrm{inv},n}, V^{\mathrm{inv},n}, \bar{v}^{\mathrm{res}}). \quad (12)$$

If $\lambda_n > 0$, the per capita growth rate of the invader will be positive in the environment set by the residents and the invader can successfully invade, and if $\lambda_n \leq 0$, the invader will not be able to invade. Note that all resident species will show up as neutrally stable ($\lambda_n = 0$) equilibria for the invader, although not necessarily attractors.

In figure 1 we depict an invasion event in the Lotka-Volterra model. For the single resident species depicted at equilibrium at the dotted line marked "invasion" we can find two invader equilibria given by

$$\bar{x}^{\mathrm{inv},1} \approx -1.81, \quad V^{\mathrm{inv},1} \approx 0.0182, \quad \lambda_1 \approx 0.0962, \quad (13a)$$

$$\bar{x}^{\mathrm{inv},2} \approx 1.81, \quad V^{\mathrm{inv},2} \approx 0.0182, \quad \lambda_2 \approx 0.0962. \quad (13b)$$

The Lotka-Volterra model is symmetric in trait space, and thus, with a single resident with $\bar{x} = 0$, we find two invaders equidistant from the middle, both with positive invasion fitness. As in adaptive dynamics, we assume that only one invasion event is allowed to happen at once, and so for this example, invader 1 was chosen at random to invade the community.

In principle, this procedure gives us an invasion criterion for a community. If there exists any invader equilibrium with $\lambda_n > 0$, we can add a species to the community at a low density with mean trait $\bar{x}^{\mathrm{inv},n}$ and trait variance $V^{\mathrm{inv},n}$. However, in practice, exhaustively proving that all such equilibria have been found is in general not feasible, so we will use a heuristic. For a given resident community we compute the invasion fitness for all invaders across a range of mean traits and with zero trait variance. This is equivalent to computing the invasion fitness landscape in adaptive dynamics. We then find all the local maxima of this adaptive dynamics fitness landscape and use those as the initial conditions for the invader moment equations (eqq. [11]) and solve the equations until they reach equilibrium. We can then compute the invasion fitness at all of these equilibria to determine whether the community is closed to invasion. While theoretically not exhaustive, we have found this heuristic to work very well in practice, as the zero-variance invaders serve as good first approximations to where positive invasion fitness might be available.

Assembly Protocol. We can now use the moment equations, the branching condition, and the invasion process to assemble an eco-evolutionarily stable community. To assemble a globally eco-evolutionarily stable community, we start with an arbitrarily specified community of S species with total densities u_i^0, mean traits $\bar{x}_i^0$, and trait variances V_i^0. We then proceed along the following steps.

1. We let the community evolve according to equations (8) until it reaches equilibrium.

2. We check each species for evolutionary branching. In case of a branching we split the species undergoing branching into two new species and then return to step 1, letting the new community of $S + 1$ species evolve according to equations (8).

3. In case the moment equations for the resident community reach equilibrium and there are no branchings, we use our invasion scheme to see whether any invader with positive invasion fitness exists. If an invader with positive invasion fitness is found, it is added to the community with a small density, and we return to step 1 and let the new community evolve once again according to equations (8).

We continue going through these steps until we have reached a community where equations (8) are in equilibrium and no more invaders with positive invasion fitness can be found. This community is thus eco-evolutionarily stable. In figure 1 we depict an example of this process for the Lotka-Volterra model. Note that at the first dotted line in figure 1, we first calculate the branching criterion, but a branching is not possible for that configuration, and we thus move on to step 3 to check for invasions.

The purpose of our algorithm is to find the final ESC. Our assembly process cannot accurately capture the temporal dynamics of the trait space equations or other assembly processes, as we integrate the moment equations to equilibrium between each branching or invasion event. Moreover, we have necessarily made some choices regarding the order in which we carry out our assembly steps. We have chosen to check for evolutionary branchings before invasions, as the existence of a branching implies a successful invasion but not vice versa. When a single final ESC exists, the order will not matter much, as the assembly process will converge on this ESC. Our Lotka-Volterra example models in this article are of this type. However, for more complicated eco-evolutionary dynamics, multiple alternate ESCs may exist, and under such conditions choices made regarding assembly order may yield different final communities. This situation is, however, no different from community assembly in adaptive dynamics, and similarly to the situation there, care must be taken when multiple ESCs are present, using tools from, for example, bifurcation theory to capture all of the possible ESCs.

Eco-Evolutionarily Stable Communities in the Unstructured Lotka-Volterra Model. We now have all the tools necessary for assembling ESCs, so we will now turn to applying them to our unstructured Lotka-Volterra model

(eqq. [10]). As we stated, the Lotka-Volterra model exhibits an inherent tension between the tendency toward multiple species and larger ITV in each species under disruptive or weak stabilizing selection. Using adaptive dynamics, where no species has any ITV, Ranjan and Klausmeier (2022) studied a similar Lotka-Volterra model and found that as the resource spectrum became wider, an increasingly large number of species could coexist in the assembled eco-evolutionarily stable community. Conversely, in another similar Lotka-Volterra model, Barabás et al. (2022) found that ITV decreased when more species were included in a quantitative genetics models for a given resource spectrum width, but had no way to systematically determine whether any of their communities were stable to invasions or evolutionary branchings. Here, we will use our moment equations together with our assembly procedure to determine how community trait variation is partitioned into inter- and intraspecific terms in our Lotka-Volterra model.

To see how this tension manifests, we assemble eco-evolutionarily stable communities for a range of different resource spectra. Specifically, we vary the resource spectrum variance V_r from 1 to 36, although for ease of interpretation we will here present results using $w_r = \sqrt{r_0 V_r}$ as the independent variable, which describes the half-width of where the net growth function $r(x)$ is positive (the fundamental community sensu Klausmeier et al. 2020). We depict the results in figure 2*A*. To further examine the role of ITV in eco-evolutionary community assembly, we also compare the results from our model with ITV to a model that does not incorporate ITV (adaptive dynamics; see sec. S3 of the supplemental PDF), depicted in figure 2*B*.

When $w_r = 1$, selection is strongly stabilizing, and only mutations prevent the trait variance of the single species from collapsing to zero. As w_r becomes wider, stabilizing selection weakens, and the disruptive selection from intraspecific competition initially increases trait variance, but eventually the one-species community becomes invasible and the community transitions into a two-species community. As we increase w_r, the ESCs with ITV initially follows the ESCs without ITV closely (fig. 2*D*). However, as w_r becomes increasingly large, the role of ITV becomes increasingly important, and the bifurcations into more species desynchronize between our model and the one without ITV (fig. 2*A*, 2*B*). In particular, the species more centrally located in trait space show large differences for when ITV is included compared with when it is not.

Figure 2*E* and figure 2*F* show two communities where our model with ITV exhibits large discrepancies compared with when ITV is not taken into account, in terms of both the number of species present in the community and the values of the mean traits. One primary reason for this discrepancy is the fact that species close to the center of the resource spectrum develop large trait variances. This is in contrast to the species closer to the edges of the resource spectrum, which have less trait variance. These differences come about through intra- and interspecific competition. As can be seen in equation (10c), intraspecific competition always generates disruptive selection, and interspecific competition can engender either stabilizing or disruptive selection, depending on how far apart the species' mean traits are. Additionally, all species are not equally prevalent, since the environmental conditions are better toward the center of trait space and the species there have larger total densities u than species close to the edge. This means that species close to the center will experience more intraspecific competition and less interspecific competition, resulting in stronger disruptive selection, which in turn translates to more standing variation in the ESC for these species. This model is thus an example of when being able to keep track of both ITV and dynamically assembling a community with a variable number of species is required for understanding how trait variation is partitioned over the long term. We also note that the substantial differences in trait variances between species in the ESCs for larger resource spectrum widths means that models that incorporate ITV but fix the trait variances would also have been insufficient for a good characterization of the distribution of traits.

Figure 2*D* and figure 2*E* show good agreement between the trait space solution (in gray) and the moment equation approximation (in black). Although qualitative agreement is usually good between the moment solution and trait space solution for the ESC (e.g., fig. 2*F*), the moment approximation becomes less accurate near transitions in species richness for the moment equation ESC. This is due to the fact that while the moment equations by construction always has a well-defined number of species, the trait space equations have no such constraints and around the transition points in species richness for the moment equations, the trait space ESCs tend to exhibit nonnormal shapes that are ambiguous with respect to the number of species. We provide examples of this in section S5 of the supplemental PDF, where assembled communities can be seen for all resource spectrum widths w_r.

The amount of standing variation in an ESC also depends on how much variation is generated through mutation (fig. 2*C*). For exceedingly low mutation variances M, the ESCs with ITV closely resemble those without ITV (fig. 2*G*). However, for the species located in the middle of trait space, even very low levels of mutation variance can result in qualitative differences, with the two central species merging around $M \approx 10^{-8}$. To better understand why this merging happens, we note that as trait variances get larger because of increased mutation widths, both the directional selection repelling the two species (eq. [10b]) and the stabilizing selection generated by interspecific competition with other species (eq. [10c]) will get weaker. This

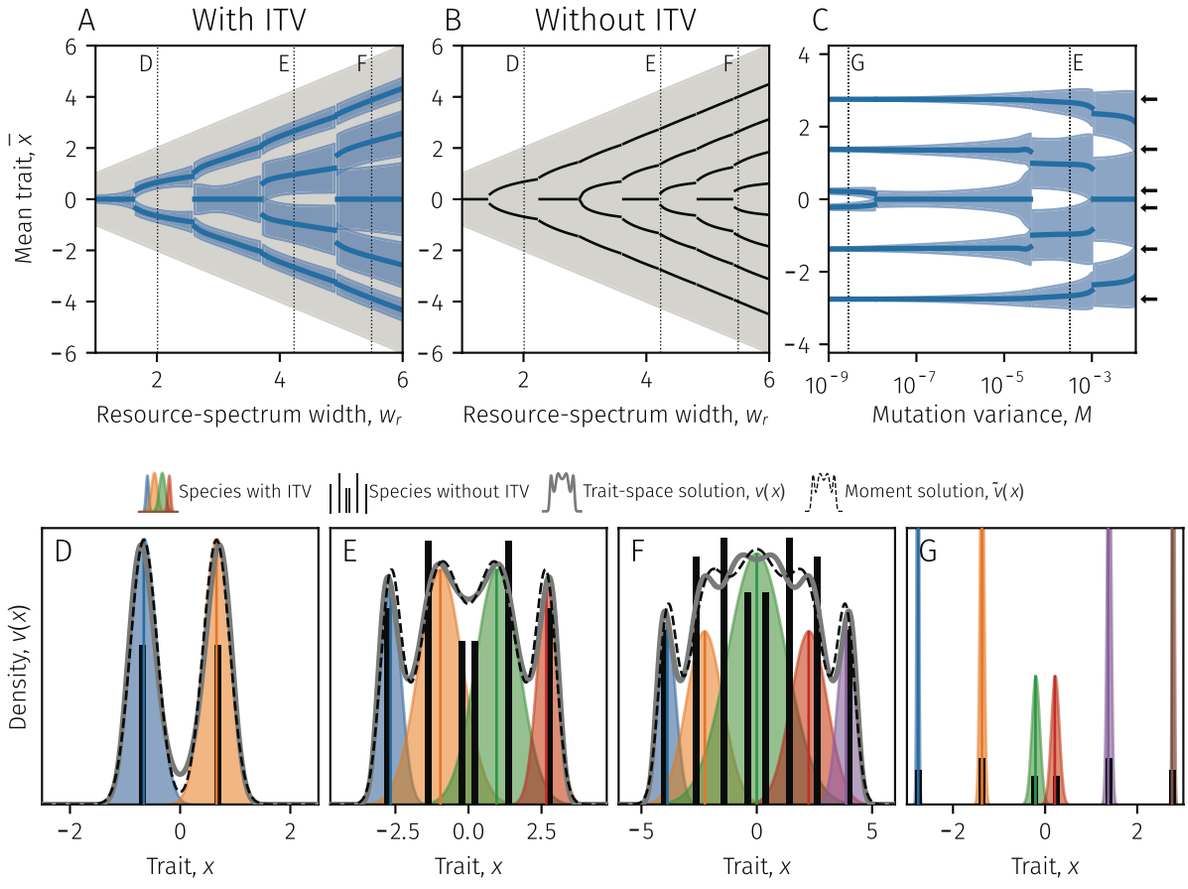

Figure 2: Eco-evolutionarily stable communities for different resource spectrum widths and mutation variances in the unstructured Lotka-Volterra model. *A*, For each value of resource spectrum half-widths ($w_r = \sqrt{r_0 V_r}$) we depict the mean traits (solid blue lines) and 1 standard deviation (filled blue areas) for each species in the eco-evolutionarily stable community computed assuming species with intraspecific trait variation (ITV) for that resource spectrum width. The gray area depicts where the environment yields positive growth rate (i.e., $r(x) \geq 0$). The mutation variance is $M = 10^{-3.5}$. *B*, Same as *A*, but black lines here depict the mean traits in eco-evolutionarily stable communities computed assuming species without ITV. *C*, For each value of mutation variance M we depict the mean traits (solid blue lines) and 1 standard deviation (filled blue areas) for each species in the eco-evolutionarily stable community for that mutation variance. Arrows on the right indicate the mean traits of the eco-evolutionarily stable communities without ITV. The resource spectrum width is $w_r \approx 4.2$. *D*–*G*, Eco-evolutionarily stable communities computed assuming species with and without ITV for the values of w_r and M indicated by dotted lines in *A*, *B*, and *C*. The gray line depicts the numerical solution of the trait space equations (eqq. [3]), $v(x)$, and the black broken line depicts the numerical solution of the moment equations (eqq. [10]), $\tilde{v}(x) = \sum_{i=1}^{S} u_i \mathcal{N}(x, \bar{x}_i, V_i)$, where the number of species S was determined through our assembly procedure. The colored areas depict the trait densities of each species $i = 1, \ldots, S$ when ITV is included, and the black bars depict the densities and traits of species when ITV is not included. Parameter values other than w_r and M are as in table 2.

will ultimately lead to the two species collapsing into one as the mutation variance gets bigger. As the mutation variance is further increased, other species will merge for the same reasons, but as stated above, more centrally located species are more sensitive to this pattern, as they experience stronger intraspecific competition.

Eco-Evolutionary Dynamics and Community Assembly in Structured Populations

For communities of unstructured populations, we saw how weakened stabilizing selection could increase both the number of species and ITV and that there was an inherent tension between these two forces. In spatially structured communities, a related phenomenon spread over space can take place. In heterogeneous environments, spatially varying selection can lead to local adaptation within a species (Kirkpatrick and Barton 1997; Bruggeman 2009; Norberg et al. 2012; Le Gland et al. 2020), resulting in greater ITV across the landscape (essentially, increased beta trait diversity within a species). On the other hand, under the no-variance conditions of adaptive dynamics, variable local conditions can lead to coexistence of multiple species (Troost et al. 2005; Débarre and Gandon 2010; Fortelius et al. 2015;

Wickman et al. 2017). Additionally, using models with fixed trait variance, large fixed variances have been shown to lead to communities with fewer surviving species but with more local adaptation, and smaller fixed variances to more surviving species but with less local adaptation (Norberg et al. 2012; Edwards et al. 2018). Thus, we here have a similar but distinct tension between ITV and diversification into multiple types, but now playing out over space in the form of local adaptation. To be able to model such scenarios, we need to generalize equation (2) to take population structure (including spatial structure) into account.

Trait Space Equations for Class-Structured Communities

Since populations can be structured in ways other than spatial, for generality we will here assume that the community is class structured, meaning that the community can be sorted into K discrete bins, such as spatial patches, age classes, or size classes. The trait density distribution in each class k is given by $v_k(x)$, $k = 1, 2, \ldots, K$, which describes how abundant individuals with a given trait x in class k are. We also write $\mathbf{v} \coloneqq (v_1, \ldots, v_K)$ for the vector of all trait density distributions. For unstructured communities it was sufficient to consider a birth rate and a mortality rate, but in general structured communities other demographic processes can cause the trait density $v_k(x)$ in each class to change over time. We can consider separately the contribution of each process with per capita rate $f(x, \mathbf{v})$ from a source class s to a destination class d. Within-class processes ($s = d$) may include local birth and mortality rates on a spatial patch, whereas between-class processes ($s \neq d$) may include immigration from spatial patch s or from births from adult class s to juvenile class d in a stage-structured model. Each such process can have a mutation kernel $\mathcal{N}(x, y, M)$ associated with it (most processes will have $M = 0$). The contribution of each process to the trait space equations is given by

$$\frac{\mathrm{d}v_d(x)}{\mathrm{d}t} \pm \int_{-\infty}^{\infty} f(y, \mathbf{v}) v_s(y) \mathcal{N}(y, x, M) \mathrm{d}y, \tag{14}$$

where the $\pm$ operator means addition to the left-hand side, so that we sum up the rates of all processes to get the total rate of change of $v_d(x)$. For (most) processes where $M = 0$, we will interpret integration of the process rate against the mutation kernel in the delta Dirac sense so that simply

$$\int_{-\infty}^{\infty} f(y, \mathbf{v}) v_s(y) \mathcal{N}(y, x, 0) \mathrm{d}y = f(x, \mathbf{v}) v_s(x). \tag{15}$$

Trait Space Equations for the Two-Patch Lotka-Volterra Model. To take a concrete example, we generalize our Lotka-Volterra competition model to take place on two patches, so that $K = 2$, with local births b_1 and b_2, deaths μ_1 and μ_2, competition a on each patch, and a constant symmetric rate of dispersal D between the patches. The trait space equations are given by

$$\frac{\mathrm{d}v_1(x)}{\mathrm{d}t} = \int_{-\infty}^{\infty} b_1(y) v_1(y) \mathcal{N}(y, x, M) \mathrm{d}y - \mu_1(x) v_1(x) - a(x, v_1) v_1(x) - D v_1(x) + D v_2(x), \tag{16a}$$

$$\frac{\mathrm{d}v_2(x)}{\mathrm{d}t} = \int_{-\infty}^{\infty} b_2(y) v_2(y) \mathcal{N}(y, x, M) \mathrm{d}y - \mu_2(x) v_2(x) - a(x, v_2) v_2(x) + D v_1(x) - D v_2(x), \tag{16b}$$

$$b_k(x) = r_0, \mu_k(x) = \frac{(x - x_k^{\mathrm{opt}})^2}{V_{\mathrm{r}}},$$

$$r_k(x) = b_k(x) - \mu_k(x) = r_0 - \frac{(x - x_k^{\mathrm{opt}})^2}{V_{\mathrm{r}}}. \tag{16c}$$

This model is locally the same as the unstructured Lotka-Volterra model (eqq. [3]) on each patch apart from the optimal traits x_1^{opt} and x_2^{opt} now potentially being different. Comparing with the generic trait space equations (eq. [14]), when patch 1 is the destination patch (eq. [16a]), we thus have five demographic processes, four for which patch 1 is the source patch—namely, b_1, $-\mu_1$, $-a$, and $-D$—and one for which patch 2 is the source patch, D. Of these, only b_1 has a nonzero mutation variance M associated with it.

Moment Equations for Class-Structured Communities

As for the unstructured community, we will assume that we can approximate each trait density distribution $v_k(x)$ in each class with a sum of S normal distributions with total density u_{ik}, mean trait $\bar{x}_{ik}$, and trait variance V_{ik} for species $i = 1, \ldots, S$ in class $k = 1, \ldots, K$, so that

$$v_k(x) \approx \tilde{v}_k(x) = \sum_{i=1}^{S} u_{ik} \mathcal{N}(x, \bar{x}_{ik}, V_{ik}). \tag{17}$$

Note that a species will exist across all classes (even if its density could be very close to zero in some) so that the species richness in each class, as well as globally, is equal to S. We define $\tilde{\mathbf{v}} = (\tilde{v}_1, \ldots, \tilde{v}_K)$ to be the vector of approximate densities. Also as for the unstructured communities we define the population-level per capita rate for a population with mean $\bar{x}$ and trait variance V to be

$$\hat{f}(\bar{x}, V, \tilde{\mathbf{v}}) = \int_{-\infty}^{\infty} f(x, \tilde{\mathbf{v}}) \mathcal{N}(x, \bar{x}, V) \mathrm{d}x. \tag{18}$$

We can now derive the moment equations for our class-structured system (see sec. S1 of the supplemental PDF), which, when summing over all demographic processes, are given by

$$\frac{\mathrm{d}u_{id}}{\mathrm{d}t} \pm \overbrace{\hat{f}(\bar{x}_{is}, V_{is}, \tilde{\mathbf{v}})}^{\text{i. population-level per capita rate}} u_{is}, \tag{19a}$$

$$\frac{\mathrm{d}\bar{x}_{id}}{\mathrm{d}t} \pm \overbrace{\frac{u_{is}}{u_{id}}}^{\text{ii. relative density weight}} \Bigg[\underbrace{V_{is} \frac{\partial \hat{f}}{\partial \bar{x}}(\bar{x}_{is}, V_{is}, \tilde{\mathbf{v}})}_{\text{iii. directional selection}} + \underbrace{\hat{f}(\bar{x}_{is}, V_{is}, \tilde{\mathbf{v}})(\bar{x}_{is} - \bar{x}_{id})}_{\text{iv. mean trait flow}} \Bigg], \tag{19b}$$

$$\begin{aligned} \frac{\mathrm{d}V_{id}}{\mathrm{d}t} \pm \overbrace{\frac{u_{is}}{u_{id}}}^{\text{ii}} \Bigg[& \underbrace{V_{is}^2 \frac{\partial^2 \hat{f}}{\partial \bar{x}^2}(\bar{x}_{is}, V_{is}, \tilde{\mathbf{v}})}_{\substack{\text{v. stabilizing/disruptive} \\ \text{selection}}} + \underbrace{\hat{f}(\bar{x}_{is}, V_{is}, \tilde{\mathbf{v}})(V_{is} - V_{id})}_{\text{vi. trait variance flow}} \\ & + \underbrace{\hat{f}(\bar{x}_{is}, V_{is}, \tilde{\mathbf{v}})(\bar{x}_{is} - \bar{x}_{id})^2}_{\substack{\text{viia. between- to within-class} \\ \text{variation}}} \\ & + \underbrace{2V_{is} \frac{\partial \hat{f}}{\partial \bar{x}}(\bar{x}_{is}, V_{is}, \tilde{\mathbf{v}})(\bar{x}_{is} - \bar{x}_{id})}_{\substack{\text{viib. class local adaptation and} \\ \text{directional selection interaction}}} \\ & + \underbrace{\hat{f}(\bar{x}_{is}, V_{is}, \tilde{\mathbf{v}})M}_{\text{viii. mutation}} \Bigg]. \end{aligned} \tag{19c}$$

Interpreting the Moment Equations for Class-Structured Communities. As noted for other moment-based frameworks (e.g., Norberg et al. 2001), in addition to being more tractable, moment equations can also be more interpretable than the trait space equations from which they are derived. We now go through the various terms and factors in the moment equations (eqq. [19]) and their interpretations. Table 1 contains a list of symbols and descriptions of the various quantities related to the class-structured trait space and moment equations.

Equation (19a) describes the rate of change of the total density u_{id} of species i in destination class d. Term i (population-level per capital rate) describes the per capita rate of process $\hat{f}$ between source class s and destination class d evaluated at the mean trait $\bar{x}_{is}$ and trait variance V_{is} of species i in the source class s. The equations capture how the total population densities of species change both due to within-class processes ($s = d$), such as local birth and death, and between-class processes ($s \neq d$), such as dispersal between patches.

Equation (19b) describes the rate of change of the mean trait $\bar{x}_{id}$ of species i in destination class d. Term ii (relative density weight) weighs contributions by the relative total densities of classes d and s, so that if the density in the destination class d is much greater than that in the source class s, the ecological processes going from s to d will have only a marginal impact on the mean trait in class d. Conversely, if the total density in the source class s is much greater than that in the destination class d, the ecological process will have a large impact on the mean trait in class d. The change of the mean trait is then governed by two terms, iii and iv. The first term, iii (directional selection), describes the effect of directional selection in the process $\hat{f}$ in class s, pushing $\bar{x}_{id}$ in the direction of maximum increase of $\hat{f}$ at a rate proportional to the trait variance of species i in class s, V_{is}. This effect comes about since the process in the source class will produce more trait density on the side of the mean in which the slope is pointing and less on the other side. The second term, iv (mean trait flow), describes how mean traits are homogenized by between-class transitions, where the rate of homogenization is governed by the per capita rate function $\hat{f}$, so that the mean trait of the destination class, $\bar{x}_{id}$, will change in the direction of the mean trait in the source class, $\bar{x}_{is}$. For within-class processes ($s = d$) we note that the relative density weight (ii) $= 1$ and the mean trait flow (iv) $= 0$, meaning that for within-class processes only directional selection (iii) is relevant. If the process under consideration is trait independent, such as for a constant dispersal rate between patches, directional selection (iii) would be equal to zero, but mean trait flow (iv) could still contribute toward changing the mean trait in class d if the mean traits in s and d differ.

Equation (19c) describes the rate of change of the trait variance V_{id} of species i in destination class d. As for the mean traits, the changes are weighted by the relative densities between class d and s, term ii. The dynamics of the trait variance then depends on five terms. The first term, v, describes stabilizing/disruptive selection resulting from the process with rate $\hat{f}$. Roughly speaking, if individuals close to the mean trait $\bar{x}_{is}$ of species i in class s contribute more than individuals away from this optimum to process $\hat{f}$, then the curvature as measured by $\partial^2 \hat{f} / \partial \bar{x}^2$ will be negative, which will contribute to a decrease in trait variances. Conversely, if individuals close to the mean contribute less, the curvature will be positive, and this will contribute toward increases in trait variances. The second term, vi (trait variance

Table 1: Quantities involved in the trait space and moment equations for class-structured communities

Symbol	Description	Definition	Label in eqq. (19)
x	Trait value		
K	Number of classes		
$v_k(x)$	Trait density distribution in class $k = 1, \dots, K$		
$\mathbf{v}$	Vector of trait density distributions	$\mathbf{v} = (v_1, \dots, v_K)$	
$f(x, \mathbf{v})$	Per capita rate of a demographic process		
M	Mutation variance associated with process f		
$\hat{f}(\bar{x}, V, \mathbf{v})$	Population-level rate for mean trait $\bar{x}$ and trait variance V for rate f	$\hat{f}(\bar{x}, V, \mathbf{v}) = \int_{-\infty}^{\infty} f(x, \mathbf{v}) \mathcal{N}(x, \bar{x}, V) \mathrm{d}x$	
S	Number of species		
$v_{ik}(x)$	Trait density distribution of species i in class k		
u_{ik}	Total density of species i in class k	$u_{ik} = \int_{-\infty}^{\infty} v_{ik}(x) \mathrm{d}x$	
$\bar{x}_{ik}$	Mean trait of species i in class k	$\bar{x}_{ik} = (1/u_{ik}) \int_{-\infty}^{\infty} x v_{ik}(x) \mathrm{d}x$	
V_{ik}	Trait variance of species i in class k	$V_{ik} = (1/u_{ik}) \int_{-\infty}^{\infty} (x - \bar{x}_{ik})^2 v_{ik}(x) \mathrm{d}x$	
$\tilde{v}_k(x)$	Approximate trait density distribution in class k	$\tilde{v}_k(x) = \sum_{i=1}^{S} u_i \mathcal{N}(x, \bar{x}_{ik}, V_{ik})$	
$\tilde{\mathbf{v}}$	Vector of approximate trait density distributions	$\tilde{\mathbf{v}} = (\tilde{v}, \dots, \tilde{v}_k)$	
d	Index of the destination class		
s	Index of the source class		
$\hat{f}(\bar{x}_{is}, V_{is}, \tilde{\mathbf{v}})$	Population-level per capita growth		i
u_{is}/u_{id}	Relative density weight		ii
$V_{is} \frac{\partial f}{\partial x}(\bar{x}_{is}, V_{is}, \tilde{\mathbf{v}})$	Directional selection		iii
$\hat{f}(\bar{x}_{is}, V_{is}, \tilde{\mathbf{v}})(\bar{x}_{is} - \bar{x}_{id})$	Mean trait flow		iv
$V_{is}^2 \frac{\partial^2 f}{\partial \bar{x}^2}(\bar{x}_{is}, V_{is}, \tilde{\mathbf{v}})$	Stabilizing/disruptive selection		v
$\hat{f}(\bar{x}_{is}, V_{is}, \tilde{\mathbf{v}})(V_{is} - V_{id})$	Trait variance flow		vi
$\hat{f}(\bar{x}_{is}, V_{is}, \tilde{\mathbf{v}})(\bar{x}_{is} - \bar{x}_{id})^2$	Between- to within-class variation		viia
$2V_{is} \frac{\partial \hat{f}}{\partial \bar{x}}(\bar{x}_{is}, V_{is}, \tilde{\mathbf{v}})(\bar{x}_{is} - \bar{x}_{id})$	Class local adaptation and directional selection interaction		viib
viia + viib	Effects of class local adaptation on variance	vii = viia + viib	vii
$\hat{f}(\bar{x}_{is}, V_{is}, \tilde{\mathbf{v}})M$	Mutation		viii

flow), homogenizes trait variance between classes, so that having trait density flow from class s to d drive the variance V_{id} of species i in class d closer to the trait variance V_{is} in class s. Terms vii (effects of class local adaptation on variance) describe the effects of variability in mean traits between classes on the trait variance within each class. In the case where the classes are spatial patches, a species having different mean traits for different patches would simply be referred to as "local adaptation," and we adapt this moniker here to the broader context of any class-structured community. Term viia (between- to within-class variation) describes how trait variances are increased by the differences in mean traits between classes, converting between-class variance into within-class variance. Term viib (class local adaptation and directional selection interaction) describes the interaction between directional selection and between-class differences in mean traits. Roughly speaking, trait variances will decrease when the mean trait difference and the selection gradient point in opposite directions and increase if they are aligned. Finally, term viii (mutation) is the contribution to trait variance from mutations in process $\hat{f}$, which will contribute toward increasing trait variances. Note that typically for most processes under consideration M would be zero, as in our Lotka-Volterra example (eqq. [16]), where only birth processes are assumed to have mutations associated with them. How much mutations contribute toward trait variance increase also depends on the rate $\hat{f}$. Thus, for example, in a system with high birth and death rates with mutations associated with births, the mutations would have a stronger impact on trait variance than in a system with low birth and death rates even if net per capita growth were the same in both systems. For within-class processes ($s = d$), the relative density weight (term ii) will be equal to 1, and only stabilizing/disruptive selection (term v) and mutations (term viii) will be nonzero, making these the only contributing factors. If the process $\hat{f}$ under consideration is trait independent, stabilizing/disruptive selection (term v) and class local adaptation and directional selection interaction (term viib) will be zero, but mutations (term viii), trait variance flow (term vi), and between- to within-class variation (term viia) may still contribute to changes in the trait variances.

Moment Equations for the Two-Patch Lotka-Volterra Model. For a specific example, we take our two-patch Lotka-Volterra model with trait space equations given by equations (16). We can, after identifying the various rates, now plug these into the generic class-structured moment equations (eqq. [19]) to yield the moment equations for the two-patch Lotka-Volterra system. Below we display the moment equations for the dynamics on patch 1; the dynamics on patch 2 are nearly identical, with patch index 1 swapped for patch index 2 as necessary:

$$\frac{\mathrm{d}u_{i1}}{\mathrm{d}t} = \Bigg[\underbrace{\left(r_0 - \frac{(\bar{x}_{i1} - x_1^{\mathrm{opt}})^2 + V_{i1}}{V_\tau}\right)}_{\text{i. } \hat{r}_1(\bar{x}_{i1}, V_{i1}) = \hat{b}_1(\bar{x}_{i1}, V_{i1}) - \hat{\mu}_1(\bar{x}_{i1}, V_{i1})} - \underbrace{\sqrt{2\pi V_c}\sum_{j=1}^{S} u_{j1}\mathcal{N}_{ij}}_{\text{i. } \hat{a}(\bar{x}_{i1}, V_{i1}, \hat{\nu}_1)}\Bigg] u_{i1}$$
$$- \underbrace{D}_{\text{i}} u_{i1} + \underbrace{D}_{\text{i}} u_{i2}, \tag{20a}$$

$$\frac{\mathrm{d}\bar{x}_{i1}}{\mathrm{d}t} = V_{i1}\Bigg[\underbrace{-\frac{2(\bar{x}_{i1} - x_1^{\mathrm{opt}})}{V_\tau}}_{\text{iii. } \frac{\partial \hat{r}_1}{\partial x}(\bar{x}_{i1}, V_{i1})} + \underbrace{\sqrt{2\pi V_c}\sum_{j=1}^{S} u_{j1}\frac{\bar{x}_{i1} - \bar{x}_{j1}}{V_{i1} + V_{j1} + V_c}\mathcal{N}_{ij}}_{\text{iii. } -\frac{\partial \hat{a}}{\partial x}(\bar{x}_{i1}, V_{i1}, \hat{\nu}_1)}\Bigg]$$
$$+ \underbrace{\frac{u_{i2}}{u_{i1}}}_{\text{ii}} \underbrace{D(\bar{x}_{i2} - \bar{x}_{i1})}_{\text{iv}}, \tag{20b}$$

$$\frac{\mathrm{d}V_{i1}}{\mathrm{d}t} = V_{i1}^2\Bigg[\underbrace{-\frac{2}{V_\tau}}_{\text{v. } \frac{\partial^2 \hat{r}_1}{\partial x^2}(\bar{x}_{i1}, V_{i1})} + \underbrace{\sqrt{2\pi V_c}\sum_{j=1}^{S} u_{j1}\frac{V_{i1} + V_{j1} + V_c - (\bar{x}_{i1} - \bar{x}_{j1})^2}{(V_{i1} + V_{j1} + V_c)^2}\mathcal{N}_{ij}}_{\text{v. } -\frac{\partial^2 \hat{a}}{\partial x^2}(\bar{x}_{i1}, V_{i1}, \hat{\nu}_1)}\Bigg]$$
$$+ \underbrace{\frac{u_{i2}}{u_{i1}}}_{\text{ii}} \underbrace{D(V_{i2} - V_{i1})}_{\text{vi}} + \underbrace{\frac{u_{i2}}{u_{i1}}}_{\text{ii}} \underbrace{D(\bar{x}_{i2} - \bar{x}_{i1})^2}_{\text{viia}} + \underbrace{r_0 M}_{\text{viii}}. \tag{20c}$$

where $\mathcal{N}_{ij} = \mathcal{N}(\bar{x}_{i1}, \bar{x}_{j1}, V_{i1} + V_{j1} + V_c)$. Here, we have marked the various terms with their corresponding terms in the generic equations (eqq. [19]). The total density dynamics (eq. [20a]) describe the local net growth on patch 1 due to the intrinsic birth and death rates, the mortality from local competition, and dispersal to and from patch 2. The mean trait dynamics (eq. [20b]) describe local selection on patch 1, where the selection due to the intrinsic growth rate drives the mean trait toward the patch 1 optimum x_1^{opt}, and the selection due to local competition drives each species mean trait apart from the mean traits of other species. The second term describes mean trait flow from patch 2 driving the mean trait on patch 1 to become more similar on patch 2, eroding local adaptation over time. The first term of the trait variance dynamics (eq. [20c]) describes local stabilizing/disruptive selection, where selection due the intrinsic growth rate is universally stabilizing and selection from local competition can be either stabilizing or disruptive in the same way as for the unstructured model. The next term describes trait variance flow, which drives the trait variance on patch 1 to become closer to the variance on patch 2. The final term describes how between-patch variation (i.e., the difference between mean traits on the patches) is converted to within-patch variation by driving an increase in variance. Note that since the only between-patch process, with rate D, is trait independent, term viib in the generic equations (eq. [19c]) does not arise in this two-patch model.

Eco-Evolutionary Community Assembly for Class-Structured Communities

Our general approach for community assembly in class-structured communities closely resembles that for

unstructured communities, albeit with more involved mathematical machinery. For evolutionary branchings, we perform the same kind of splitting and stability analysis as for the unstructured communities. The invasion analysis too proceeds along similar lines, but since the community is now structured we need to keep track of the frequency distribution of invaders across classes. As for the unstructured model, we can use these branching and invasion criteria to build up a community one species at a time until no more invasions or branchings are possible and we have an eco-evolutionarily stable community. The details of how the branching and invasion analysis are carried out for structured communities are available in section S2 of the supplemental PDF.

Eco-Evolutionarily Stable Communities in the Two-Patch Lotka-Volterra Model

When the optimal traits on the patches x_1^{opt} and x_2^{opt} differ between the patches, there will be local selection toward different traits on the two patches (eq. [20b]). Under sufficiently low dispersal a single species can thus be expected to exhibit local adaptation, with its mean trait differing between patches. However, based on insights derived from adaptive dynamics, we expect to instead see multiple species as a response to heterogeneous local conditions. This then raises the question when these two possibilities are combined: with heterogeneous local conditions and weak dispersal, will we end up with fewer locally adapted species or more species with less local adaptation but differing in their mean traits?

In the two-patch Lotka-Volterra model (eqq. [20]) as well as the general class-structured moment equations (eqq. [19]), we can see that directional selection (term iii) is multiplied by the within-patch trait variance of the species to determine the effect of directional selection on changes in the mean trait. We can also see that there is a term that converts between-patch variation into within-patch variation (term viia). This means that if the trait optima on the two different patches are different, there will be selective pressure for the mean traits in a species to separate, and as they separate, term viia will increase within-class variation, strengthening local directional selection and further increasing the selective pressure on trait separation. This, then, creates a positive feedback between local adaptation (between-class variation) and within-class variation. However, the potential of local adaptation as a strategy for covering more of trait space on the regional scale has two limitations potentially opening up a locally adapted species to invasion. First, the mean trait flow term (iv) acts as a barrier to local adaptation by exerting a force toward mean trait homogenization and may prevent sufficient local adaptation from developing, leaving unused trait space available for invasion. Conversely, if local adaptation—and hence within-patch trait variance—becomes too large, this might make the species relatively maladapted by covering too much unfavorable trait space, again opening up the species to invasion. None of these scenarios are universally favored above another, and local adaptation, multiple species, or neither will be model and parameter dependent.

To explore a specific instance of this tension between local adaptation and divergence into multiple species, we use our Lotka-Volterra model (eqq. [20]) and assemble eco-evolutionarily stable communities under conditions of weak dispersal and for a range of differences in the trait optima between the two patches. Specifically, we let $V_r = 4$ on each patch, which is enough resource spectrum breadth for two species to coexist in the unstructured model, and then make the patches more dissimilar by varying $x_2^{\text{opt}} = -x_1^{\text{opt}}$ from 0 to 2. The results are depicted in figure 3, and parameter values are listed in table 2.

Generally, the outcomes when we vary the patch dissimilarity fall into three categories with respect to local adaptation. The first is no local adaptation (e.g., fig. 3*E*, 3*F*). The second is symmetric local adaptation, meaning that a species is split roughly equally between the two patches and the mean traits between the patches differ (e.g., fig. 3*C*). The third is asymmetric local adaptation, where species are significantly more prevalent on one patch, and their mean trait on the sink patch differs from that of the main patch (e.g., fig. 3*D*). To better illustrate the effects of the inclusion of ITV, we also depict ESCs for a model that does not incorporate ITV (adaptive dynamics; see sec. S3 of the supplemental PDF). Note that without ITV, all individuals in a species are identical, meaning that a species necessarily has the same mean trait on both patches. Below we describe in detail how the ESCs change as the patch optima become further separated.

When the optima are both equal to zero, the patches are identical and the two-patch system is functionally equivalent to an unstructured model. Conversely, when the optima are equal to ± 2 there is no overlap in trait space of positive growth rates between the two patches, and for any species having a positive intrinsic net growth rate on one patch, the other patch will be a pure sink. To the very left in figure 3*A* and 3*B* the communities with and without ITV agree in terms of mean traits, and since the patches are identical, two species exist across the region. However, after the patch optima separate only slightly, the community without ITV diverges into a four-species system, with two species roughly corresponding to the community that would have evolved on patch 1 in isolation and one community corresponding to the one that would have evolved on patch 2 in isolation. In contrast, the communities with ITV remain as a two-species system all the way up to roughly

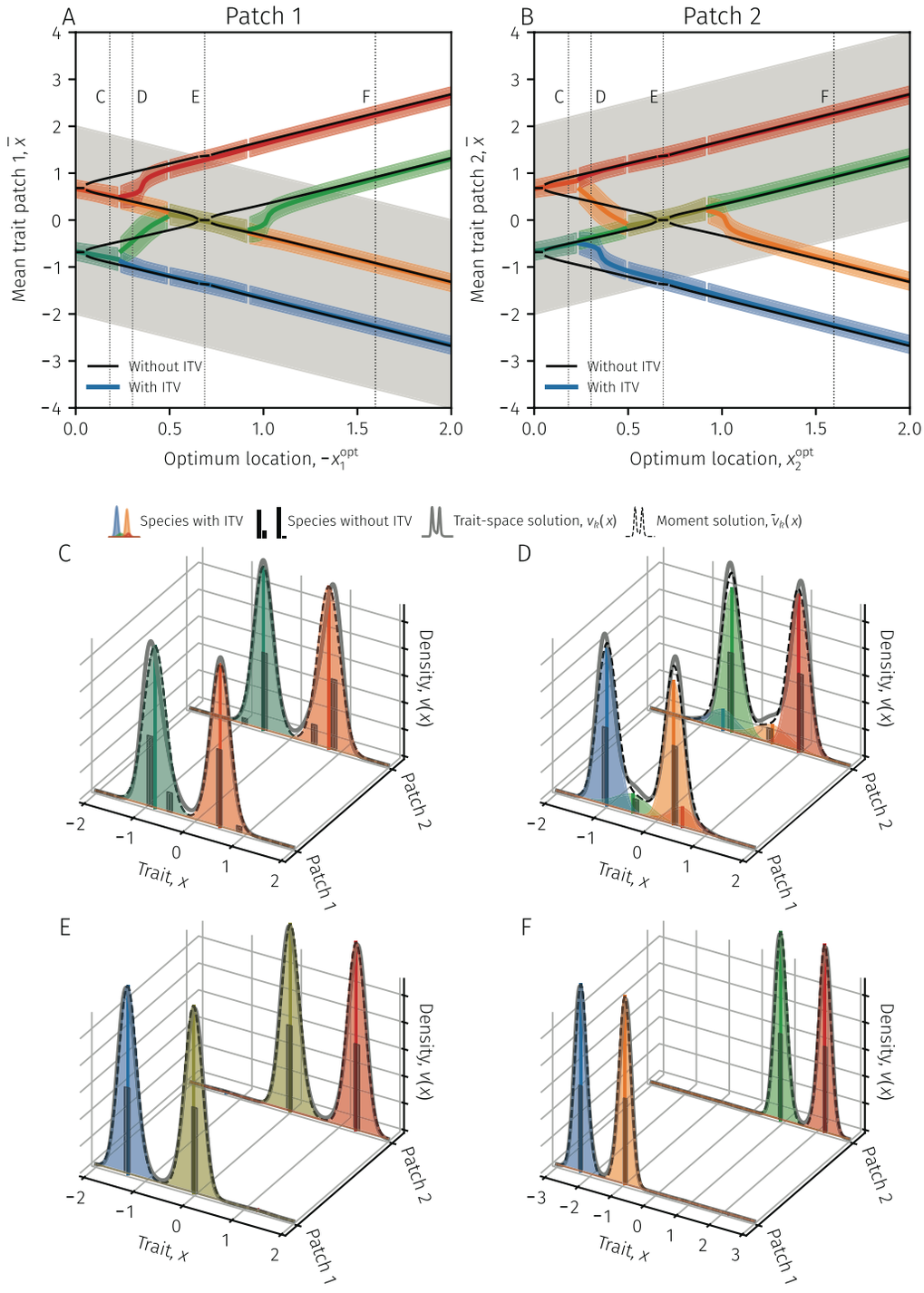

Figure 3: Eco-evolutionarily stable communities for different environmental optima in the two-patch Lotka-Volterra model. *A*, *B*, For each value of environmental optima x_1^{opt} and x_2^{opt} we depict the mean traits (solid colored lines) and 1 standard deviation (filled colored areas) for each species in the eco-evolutionarily stable community computed assuming species with intraspecific trait variation (ITV) for that pair of optima. Depicted as black lines are the eco-evolutionarily stable communities for communities computed assuming species without ITV. Note that without ITV, local adaptation is precluded, and these black lines are the same in *A* and *B*. The gray area depicts where the environment yields positive growth rate (i.e., $r_k(x) \geq 0$) on patch 1 (*A*) and patch 2 (*B*). The species in the communities with ITV are color coded so that the same species is depicted in the same color for both patches for any given value of x_k^{opt}. *C*–*F*, Eco-evolutionarily stable communities for the values of x_k^{opt} indicated by the dotted lines in *A* and *B*. The gray line depicts the numerical solution of the trait space equations (eqq. [16]), $v_k(x)$, and the black broken line depicts the numerical solution of the moment equations (eqq. [20]), $\tilde{v}_k(x) = \sum_{i=1}^{S} u_{ik} \mathcal{N}(x, \bar{x}_{ik}, V_{ik})$, where the number of species S was determined through our assembly procedure. The colored areas depict the trait density of each species $i = 1, \ldots, S$ for the moment equations, and the black bars depict the traits and densities of the eco-evolutionarily stable community without ITV. Parameter values are as in table 2.

Table 2: Parameters for the two Lotka-Volterra models

Symbol	Description	Value/range	
		Unstructured	Two patch
r_0	Maximal growth rate	1	1
V_r	Resource spectrum variance	[1, 36]	4
V_c	Competition variance	1	1
M	Mutation variance	$10^{-3.5}$	10^{-4}
x_1^{opt}	Optimal trait, patch 1	...	[−2, 0]
x_1^{opt}	Optimal trait, patch 2	...	[0, 2]
D	Dispersal rate	...	10^{-3}

$x_k^{opt} = \pm 0.25$, but with both species exhibiting symmetric local adaptation between the patches (fig. 3*C*).

The community with ITV does split into four species around $x_k^{opt} = \pm 0.25$, but the resulting four-species community is still characterized by significant asymmetric local adaptation in at least two species for the interval between approximately $0.25 \leq \pm x_k^{opt} \leq 0.5$ (fig. 3*D*). The two species depicted in blue and orange are here primarily patch 1 specialists, and the species depicted in green and red are primarily patch 2 specialists. The asymmetry in local adaptation can come about through the weighted effect of densities on mean trait flow between the patches (terms ii and iii in eqq. [20]), where the species density on the off patch exerts relatively little pressure on the mean trait on the main patch to diverge from its local optimum.

Around $x_k^{opt} = \pm 0.7$ the two sets of lines describing the community without ITV on each patch cross, and there is a small interval where the community without ITV will have only three species before the lines separate after the cross into four species again. For the community with ITV, the interval with three species is significantly larger, spanning roughly $0.5 \leq \pm x_k^{opt} \leq 0.9$. For this interval, the community is characterized by two outer species (blue and red) with little local adaptation and a central species (olive) that exhibits significant and symmetrical local adaptation except in the middle of the interval, where there is no significant local adaptation in any of the three species (fig. 3*E*).

After $x^{opt} = \pm 0.9$ the community with ITV once again splits into four species, where the central two species (orange and green) are initially characterized by asymmetrical local adaptation. As the environmental optima separate further the means converge onto those for the community without ITV, and for large separations $|x_k^{opt}| > 1.1$ the system for both the communities with and without ITV are characterized by two species (blue and orange) being present almost entirely on patch 1 and two species (green and red) being present almost entirely on patch 2 (fig. 3*F*). Because of the huge asymmetry in densities across the two patches, the mean trait flow from the main patch to the sink patch becomes so strong that local adaptation can effectively not occur on the sink patch.

Across the range of patch dissimilarities, this model then showcased a range of behaviors with respect to local adaptation and diversification into multiple species. That we could roughly sort these outcomes into three qualitatively different regimes is particularly interesting, and we could not have come across this behavior without the use of our framework.

As for the unstructured model, the two-patch moment equation ESCs mostly have good agreement with the trait space equations, with some issues around the transition points in the number of species (see sec. S5 of the supplemental PDF). One issue that did not arise in the unstructured model is that very close to the transition from two to four species ($x_k^{opt} \approx \pm 0.25$), the two-species community depicted is invasible, but after the invasion, one of the original species is depressed to extinction, after which the invader assumes the total density, mean, and variance of the extinct resident, yielding a never-ending cycle of invasions and extinctions. Similarly, the species are also branchable, but after an initial divergence in trait space one of the branching species becomes extinct and the remaining species assumes the distribution of the original branched resident, yielding a never-ending branching-extinction cycle. For these kind of cycles, we have amended our assembly procedure to remove any species with very low total densities and to merge any species whose mean traits and trait variances are very close before any branchings or invasions are checked for. We define the ESC to be the community to which the cycle returns between branchings or invasions that is in equilibrium with respect to equations (19), which is the community we depict in figure 3*A* and 3*B* for $x_k^{opt} \approx \pm 0.25$. This cycling phenomenon occurs only in a very small sliver of parameter space.

Generalizing the Framework

For the purposes of exposition and to focus on our main questions regarding the tension among ITV, local

adaptation, and diversification into multiple species, we have kept our example models simple. However, several more complications can be handled by generalizing the framework. First, more than one trait may affect performance, so tracking a single scalar trait may not always be sufficient, and in such cases we would need some way of deriving the dynamics for a mean trait vector and a trait variance-covariance matrix. In sections S1 and S2 of the supplemental PDF we show how the framework can be expanded to include multiple traits in this way. Second, in our Lotka-Volterra models the rate functions were simple enough that we could calculate the population-level rates necessary for the moment equations using Gaussian integration analytically. This will in general not be possible, and in section S1.3 of the supplemental PDF we show how to derive Taylor approximations of arbitrary order to accommodate such situations. Third, our Lotka-Volterra models do not include any dependence on any external variables, such as abiotic resources, and in section S1.5 of the supplemental PDF we show how external variables can be included in the framework. To provide an example that includes all of these complications, we have in section S4 of the supplemental PDF briefly explored a stage-structured model with one juvenile and one adult stage in two traits that compete for two abiotic resources.

We have here focused on fully heritable trait variation, but our framework can be extended to include nonheritable environmental variation. While we have not worked this case out to the same level of generality as we have for fully heritable traits, in section S1.6 of the supplemental PDF we provide a sketch for the simplest case of one trait in unstructured populations. While it is relatively straightforward to incorporate the generation of nonheritable variation into the model, it requires additional moment equations, and the derivation of the moment equations from the trait space equations becomes more involved.

Discussion

In this article, we have presented a general framework for eco-evolutionary community assembly for class-structured communities that incorporates ITV. We have done so by deriving moment equations for the total density, mean trait, and trait variance for each species in a community, combined with a procedure for determining whether additional species need to be added to a community in order for it to be closed to further invasion. Through examples, we demonstrated the application of the framework in an unstructured and a two-patch-structured Lotka-Volterra competition model, where we saw how less stabilizing conditions could result in different combinations of more intraspecific variation, local adaptation, and the addition of more species to the assembled eco-evolutionarily stable community.

Intra- and Interspecific Trait Variation

In recent years, the role of intraspecific vs. interspecific variation in traits has received increasing attention in functional and community ecology, with two broad questions at the center. First, how much of trait variation is intraspecific and how much is interspecific (Albert et al. 2011; Siefert et al. 2015; Griffiths et al. 2016; Gaudard et al. 2019; Xavier Jordani et al. 2019)? And second, how important is ITV for higher-level outcomes such as species coexistence and ecosystem functioning (Bolnick et al. 2011; Violle et al. 2012; Turcotte and Levine 2016; Raffard et al. 2019)?

Regarding the first question, ITV has in general been found to account for substantial portions of trait variation, especially in plants (Siefert et al. 2015; Westerband et al. 2021). However, in some study systems of ants (Gaudard et al. 2019) and beetles (Griffiths et al. 2016) ITV was found to be negligible, and even among plant studies the preponderance of ITV is highly variable (Westerband et al. 2021); in addition, patterns of intra- and interspecific variation can be highly idiosyncratic (Costa-Pereira et al. 2018; Umaña and Swenson 2019). For the insect-plant discrepancy, Gaudard et al. (2019) suggested that one explanation could be related to the higher plasticity in plants that arises as a consequence of plants being sessile. In the context of individual niche specialization, several factors have been proposed as important for accounting for the level of ITV, including intra- and interspecific competition, ecological opportunity (the diversity of resources), and predation (Araújo et al. 2011). While these factors can no doubt play a role in shaping ITV, they can also, in turn, be shaped by ITV. In our unstructured Lotka-Volterra model (eqq. [10]; fig. 2) ecological opportunity can roughly be said to correspond to the resource spectrum width w_r, which we take to be fixed, but intra- and interspecific competition both shape and are shaped by intra- and interspecific trait variation through eco-evolutionary feedbacks, so that neither can be said to be the strict cause of the other. In field studies, idiosyncratic patterns of trait variation are to some extent to be expected because of the myriad factors that can be present in natural systems. Interestingly, however, even for our simple model with just one parameter varied (fig. 2*A*), ITV is sometimes, but not always, important for characterizing the trait variation in the community. When the width of the resource spectrum is small, yielding one or two species ($w_r \leq 2.3$), ITV is small so the trait means of the species of our model incorporating ITV agree very well with a model not incorporating ITV, implying that ITV is not important for characterizing the trait distribution in the community. For larger resource spectrum widths, however, ITV becomes much more substantial, and the mean trait values—and even the number of species in the community—no longer agree with the model without ITV,

implying that the role of ITV is crucial for characterizing the trait distribution in the community. Given the simplicity of our model, our results thus suggest that whether ITV is important for characterizing communal trait variation could be highly system specific and may resist broad-scale explanation. However, a more complete theoretical exploration of whether broad patterns in different models can be found that serve as good indicators for the importance of ITV is outside the scope of this article, and more research will be required to determine the extent to which such patterns exist. Our framework would serve as a good tool for carrying out such explorations.

Scaling up to structured communities, Albert et al. (2011) proposed that in a nested sampling design, ITV should saturate as the spatial or ecological scale is increased, since at a sufficiently large scale species will cover their entire range, meaning that interspecific trait variation should become the more important factor. Although our two-patch Lotka-Volterra model (eqq. [20]; fig. 3) is not set up for one-to-one comparisons with this hypothesis, we observe some related phenomena as the environments on the two patches become increasingly different (fig. 3). Initially, ITV, mostly in the form of local adaptation, increases as the patches separate. More interspecific variation is then added as more species join the community, but beyond a certain point the patches are too different to permit local adaptation and interspecific variation dominates. To wit, not much theoretical attention has been paid to what conditions generically promote intra- versus interspecific variation on the regional scale (but see Norberg et al. 2012; Edwards et al. 2018), and a more systematic exploration of this question would be an interesting application of our framework.

Regarding the second question concerned with how ITV affects higher-level outcomes, species coexistence has been proposed to be both negatively and positively related to ITV (Violle et al. 2012). In two theoretical models of competition with fixed intraspecific variances, Hart et al. (2016) and Barabás and D'Andrea (2016) found that coexistence is (mostly) hampered by ITV. In our framework, both the number of species and ITV are dynamic outcomes, and it is thus not strictly possible to speak causally about how species coexistence affects ITV or vice versa within the framework. As we have done, however, it is possible to compare a model that includes ITV (our framework) to one that does not (adaptive dynamics), and in this sense it seems unlikely that the inclusion of ITV would yield a higher number of coexisting species. The available trait space must be apportioned, and if it can be effectively covered by fewer species by incorporating ITV, the number of coexisting species will be lower.

In a two-patch version of the Hart et al. (2016) model, Uriarte and Menge (2018) found that ITV could promote regional species coexistence. This contradicts our findings, and in our two-patch model, ITV in the form of local adaptation can preclude the coexistence of species by a single species covering more trait space. A crucial difference between our models is that Uriarte and Menge (2018) assumed that the trait means and variances were fixed on each patch, whereas in our models these are outcomes of the dynamics. As for the unstructured case, it is hard envisioning a scenario using our model where the inclusion of intraspecific variance would lead to more coexisting species than the reference model without ITV. A scenario like that of Uriarte and Menge (2018) is more likely if trait variation is plastic and driven by the environment as opposed to heritable. The nature of ITV could thus be an important factor too in determining whether ITV can promote coexistence, as has also been observed in an apparent competition model (Schreiber et al. 2011).

Ecosystem functioning has also been shown to depend on the trait distributions of communities (Mouillot et al. 2011; Gross et al. 2017). Our modeling framework opens the door for theoretical explorations of the relationship between trait variation both within and between species and various ecosystem functions. Similarly to coexistence, ecosystem function and trait variation are both outcomes of the system's dynamics, so that neither is the strict cause of the other. However, this enables explorations of what mechanisms and environments create and sustain either, neither, or both of trait diversity and ecosystem functioning.

Relationship to Other Theoretical Approaches

Our framework builds on and connects to several other strands of eco-evolutionary theory. Considering a single class and setting all mutations to zero, our framework reduces to the community ecology framework of Wirtz and Eckhardt (1996) and Norberg et al. (2001), where the moments of the trait distribution of an ensemble of species is tracked. This approach often includes an immigration term from a fixed species pool to maintain trait variance in the community. Such an immigration term could easily be incorporated into our framework by designating one of the classes a "species pool class" and letting the internal rates of this class all be zero to keep the species pool fixed. Note that our formulation also includes cases where the species pool too consists of structured populations, so that, for example, juveniles and adults in a stage-structured model could immigrate at different rates from the species pool.

Although the assumptions going into the model at the outset are different, the moment equations derived for our model are also very similar to the equations derived under the assumptions of quantitative genetics. Assuming a single class, no mutations, and that phenotypic variation equals genetic variation (no environmental variation), our

equations mirror those of Barabás et al. (2022), who derived equations for mean traits and trait variance-covariance under the assumptions of quantitative genetics for multiple traits. These similarities between trait space approaches and quantitative genetics have been noted before (e.g., Débarre et al. 2013), and the two approaches have complementary strengths and weaknesses. Most notably, the assumptions of normality are less ad hoc in quantitative genetics, and each species is, as described by a normal distribution, well defined (Turelli and Barton 1994; Barton et al. 2017). Similarly, the reproductive isolation of species, which in our moment equations is an approximation, is in quantitative genetics based on the biological species concept. This, however, comes at the cost that diversification into multiple peaks cannot be easily incorporated, as opposed to our approach here.

Our moment equations also closely resemble those derived in trait diffusion approaches (Merico et al. 2014; Le Gland et al. 2020), where mutations are generated by a diffusion process in trait space. Merico et al. (2014) derived the moment equations for well-mixed, single-species, single-trait populations, and Le Gland et al. (2020) extended this to multiple traits and spatial structure by way of reaction-diffusion equations in continuous space. For mutation kernels with small variance-covariance matrices without covariances, our mutation convolution integral is well approximated by such trait diffusion processes (Kimura 1965; Débarre et al. 2013), and our assembly framework is easily adapted to this setting, equipping the trait diffusion approaches with a way of assembling eco-evolutionarily stable communities of several species.

Finally, our framework also produces similar equations to those in oligomorphic dynamics (Sasaki and Dieckmann 2011; Débarre et al. 2014; Lion et al. 2022), where a trait density distribution is also decomposed into a number of "species" to track their moments. Compared with oligomorphic dynamics, the major innovation we present here is our invasion analysis and community assembly framework, but there are also differences in how the moment equations are derived. First, we assume that mutations are associated with some specific ecological process (typically births), whereas in oligomorphic dynamics mutations are assumed to be an independent process. Second, rather than assuming that each species is reproductively isolated, in oligomorphic dynamics it is instead assumed that new individuals are allocated to each species in proportion to each species' density for any given trait. For structured populations, additional assumptions are required (Lion et al. 2022). These assumptions do, however, ultimately produce the same general shapes for the moment equations as we derived here. Finally, rather than assuming that each species is normally distributed, oligomorphic dynamics assumes a small variance approximation and can derive equations for an arbitrary set of moments under these assumptions. To get a closed system of moment equations a so-called moment closure approximation is then used, where using normal distributions is one such possible closure.

Our choice of approximating each species' trait density as a normal distribution at the outset rather than expanding around the mean of each species for an arbitrary number of moments has both advantages and disadvantages. The advantages are that our moment equations are more stable when variances become large compared with a small variance expansion and that we can more easily integrate mutations into birth processes. The disadvantage is that the flexibility in shape is more limited. In principle, functions other than normal distributions could be used to derive the moment equations. For example, Klauschies et al. (2018) and Cropp and Norbury (2021) used beta distributions as the approximating distribution to close their moment equations, and there are also approaches that use more involved methods for making nonnormal approximations for the trait space distributions at equilibrium (Mirrahimi and Gandon 2020) as well as studies that have examined the effects of higher moments, such as skew (Débarre et al. 2015). Assumptions other than normality are likely possible while still retaining the core features of our approach, but each such differing assumption would require the rederivation of nearly all moment equations. While a shortcoming, our comparisons between the trait space equations and moment equations indicate that as long as normality in the distributions of birthed phenotypes from a parent phenotype is assumed, then our additional assumption that species' trait distributions are normal seem not to affect the accuracy of the moment approximations by any large degree, as our eco-evolutionarily stable communities assembled by moment equations agreed very well with the corresponding trait space equations (figs. *2*D–2*F*, 3*C*–3*F*). We note that although we assume normality in each species, the community trait density distribution is the sum of these normals, which makes the community distribution much more flexible (for an example, see fig. 3*D*). The primary exception to good accuracy in the moment equations is when the number of species is ambiguous. In these instances the trait space equations would yield solutions that could not easily be approximated by a sum of normal distributions that were assumed to be reproductively isolated (for examples, see sec. S5 of the supplemental PDF).

While these drawbacks should be kept in mind, we nevertheless believe that our framework makes substantial progress in eco-evolutionary modeling with ITV. In a phytoplankton model, Peeters and Straile (2018) compared trait space equations without mutations to single-species moment equations and concluded that single-species moment equations failed to provide any useful information

when considering parts of parameter space where the trait space equations diverged into multiple species. In a similar model using the trait diffusion approach, Le Gland et al. (2020) noted that their trait space equations sometimes exhibited multimodality and speculated on the utility of modeling multiple modes, making the selection of how many modes to include based on functional groups. While multispecies moment models are not new (Sasaki and Dieckmann 2011; Norberg et al. 2012; Barabás and D'Andrea 2016), our assembly approach obviates the need for a priori decisions on how many modes or species to include by using our assembly process. It also gives an alternate approach for deriving the equations for moment dynamics for general class-structured populations, compared with Lion et al. (2022).

Taken together, we believe that our framework of unifying the community assembly techniques of adaptive dynamics with the moment equation approach to including ITV could be of great use to theoreticians and modelers seeking to take advantage of facets of both eco-evolutionary modeling frameworks. We also believe that being able to assemble eco-evolutionarily stable communities that accounts for ITV could help address many ecological questions regarding the extent and importance of intra- and interspecific trait variation.

Note

Readers of this article may be interested in the work by Lion et al. (2022), who independently derived a related formalism to analyze eco-evolutionary dynamics in structured populations.

Acknowledgments

This project was funded by National Science Foundation grant DEB-1754250 to E. Litchman and C.A.K. We thank Florence Débarre, Sébastien Lion, Elena Litchman, Bob Week, the editors, and one anonymous reviewer for their comments on the work. This is W. K. Kellogg Biological Station contribution 2330.

Statement of Authorship

J.W., T.K., and C.A.K. conceived and designed the study. J.W. performed the mathematical and numerical analysis with input from T.K. and C.A.K. J.W. drafted the manuscript with comments from T.K. and C.A.K.

Data and Code Availability

Code for running the simulations and reproducing the figures is available in the Dryad Digital Repository (https://doi.org/10.5061/dryad.sqv9s4n72; Wickman et al. 2022).

Literature Cited

Albert, C. H., F. Grassein, F. M. Schurr, G. Vieilledent, and C. Violle. 2011. When and how should intraspecific variability be considered in trait-based plant ecology? Perspectives in Plant Ecology, Evolution, and Systematics 13:217–225.

Albert, C. H., W. Thuiller, N. G. Yoccoz, A. Soudant, F. Boucher, P. Saccone, and S. Lavorel. 2010. Intraspecific functional variability: extent, structure and sources of variation. Journal of Ecology 98:604–613.

Araújo, M. S., D. I. Bolnick, and C. A. Layman. 2011. The ecological causes of individual specialisation. Ecology Letters 14:948–958.

Barabás, G., and R. D'Andrea. 2016. The effect of intraspecific variation and heritability on community pattern and robustness. Ecology Letters 19:977–986.

Barabás, G., C. Parent, A. Kraemer, F. Van de Perre, and F. De Laender. 2022. The evolution of trait variance creates a tension between species diversity and functional diversity. Nature Communications 13:2521.

Barton, N., A. Etheridge, and A. Véber. 2017. The infinitesimal model: definition, derivation, and implications. Theoretical Population Biology 118:50–73.

Bolnick, D. I., P. Amarasekare, M. S. Araújo, R. Bürger, J. M. Levine, M. Novak, V. H. Rudolf, S. J. Schreiber, M. C. Urban, and D. A. Vasseur. 2011. Why intraspecific trait variation matters in community ecology. Trends in Ecology and Evolution 26:183–192.

Brännström, Å., J. Johansson, and N. von Festenberg. 2013. The hitchhiker's guide to adaptive dynamics. Games 4:304–328.

Bruggeman, J. 2009. Succession in plankton communities: a trait-based perspective. PhD thesis. Vrije Universiteit, Amsterdam.

Bürger, R. 1986. On the maintenance of genetic variation: global analysis of Kimura's continuum-of-alleles model. Journal of Mathematical Biology 24:341–351.

Champagnat, N. 2003. Convergence of adaptive dynamics *n*-morphic jump processes to the canonical equation and degenerate diffusion approximation. Prépublication de l'Université de Nanterre (Paris X) no. 3.

Champagnat, N., R. Ferrière, and S. Méléard. 2006. Unifying evolutionary dynamics: from individual stochastic processes to macroscopic models. Theoretical Population Biology 69:297–321.

Costa-Pereira, R., V. H. W. Rudolf, F. L. Souza, and M. S. Araújo. 2018. Drivers of individual niche variation in coexisting species. Journal of Animal Ecology 87:1452–1464.

Cropp, R., and J. Norbury. 2021. Modelling the evolution of naturally bounded traits in a population. Theoretical Ecology 14:255–268.

Débarre, F., and S. Gandon. 2010. Evolution of specialization in a spatially continuous environment. Journal of Evolutionary Biology 23:1090–1099.

Débarre, F., S. L. Nuismer, and M. Doebeli. 2014. Multidimensional (co)evolutionary stability. American Naturalist 184:158–171.

Débarre, F., O. Ronce, and S. Gandon. 2013. Quantifying the effects of migration and mutation on adaptation and demography in spatially heterogeneous environments. Journal of Evolutionary Biology 26:1185–1202.

Débarre, F., S. Yeaman, and F. Guillaume. 2015. Evolution of quantitative traits under a migration-selection balance: when does skew matter? American Naturalist 186(suppl.):S37–S47.

Dercole, F., and S. Rinaldi. 2008. Analysis of evolutionary processes: the adaptive dynamics approach and its applications. Princeton Series in Theoretical and Computational Biology. Princeton University Press, Princeton, NJ.

Dieckmann, U., and M. Doebeli. 1999. On the origin of species by sympatric speciation. Nature 400:354–357.

Dieckmann, U., and R. Law. 1996. The dynamical theory of coevolution: a derivation from stochastic ecological processes. Journal of Mathematical Biology 34:579–612.

Edwards, K. F., C. T. Kremer, E. T. Miller, M. M. Osmond, E. Litchman, and C. A. Klausmeier. 2018. Evolutionarily stable communities: a framework for understanding the role of trait evolution in the maintenance of diversity. Ecology Letters 21:1853–1868.

Fortelius, M., S. A. H. Geritz, M. Gyllenberg, and J. Toivonen. 2015. Adaptive dynamics on an environmental gradient that changes over a geological time-scale. Journal of Theoretical Biology 376:91–104.

Gaudard, C. A., M. P. Robertson, and T. R. Bishop. 2019. Low levels of intraspecific trait variation in a keystone invertebrate group. Oecologia 190:725–735.

Geritz, S. A. H., E. Kisdi, G. Meszéna, and J. A. J. Metz. 1998. Evolutionarily singular strategies and the adaptive growth and branching of the evolutionary tree. Evolutionary Ecology 12:35–57.

Griffiths, H. M., J. Louzada, R. D. Bardgett, and J. Barlow. 2016. Assessing the importance of intraspecific variability in dung beetle functional traits. PLoS ONE 11:e0145598.

Gross, N., Y. L. Bagousse-Pinguet, P. Liancourt, M. Berdugo, N. J. Gotelli, and F. T. Maestre. 2017. Functional trait diversity maximizes ecosystem multifunctionality. Nature Ecology and Evolution 1:0132.

Hart, S. P., S. J. Schreiber, and J. M. Levine. 2016. How variation between individuals affects species coexistence. Ecology Letters 19:825–838.

Kimura, M. 1965. A stochastic model concerning the maintenance of genetic variability in quantitative characters. Proceedings of the National Academy of Sciences of the USA 54:731–736.

Kirkpatrick, M., and N. H. Barton. 1997. Evolution of a species' range. American Naturalist 150:1–23.

Klauschies, T., R. M. Coutinho, and U. Gaedke. 2018. A beta distribution-based moment closure enhances the reliability of trait-based aggregate models for natural populations and communities. Ecological Modelling 381:46–77.

Klausmeier, C. A., C. T. Kremer, and T. Koffel. 2020. Trait-based ecological and eco-evolutionary theory. Pages 161–194 *in* K. S. McCann and G. Gellner, eds. Theoretical ecology: concepts and applications. Oxford University Press, Oxford.

Kraft, N. J. B., G. M. Crutsinger, E. J. Forrestel, and N. C. Emery. 2014. Functional trait differences and the outcome of community assembly: an experimental test with vernal pool annual plants. Oikos 123:1391–1399.

Kremer, C. T., and C. A. Klausmeier. 2013. Coexistence in a variable environment: eco-evolutionary perspectives. Journal of Theoretical Biology 339:14–25.

Lande, R. 1979. Quantitative genetic analysis of multivariate evolution, applied to brain:body size allometry. Evolution 33:402–416.

Lande, R., and S. J. Arnold. 1983. The measurement of selection on correlated characters. Evolution 37:1210–1226.

Le Gland, G., S. M. Vallina, S. L. Smith, and P. Cermeño. 2020. Spead 1.0—a model for simulating plankton evolution with adaptive dynamics in a two-trait continuous fitness landscape applied to the Sargasso Sea. Geoscientific Model Development Discussions 2020:1–54.

Levins, R. 1962. Theory of fitness in a heterogeneous environment. I. The fitness set and adaptive function. American Naturalist 96:361–373.

Lin, W.-H., E. Kussell, L.-S. Young, and C. Jacobs-Wagner. 2020. Origin of exponential growth in nonlinear reaction networks. Proceedings of the National Academy of Sciences of the USA 117:27795–27804.

Lion, S., M. Boots, and A. Sasaki. 2022. Multimorph eco-evolutionary dynamics in structured populations. American Naturalist 200:345–372.

Lotka, A. J. 1925. Elements of physical biology. Williams & Wilkins, Baltimore, MD.

MacArthur, R., and R. Levins. 1964. Competition, habitat selection, and character displacement in a patchy environment. Proceedings of the National Academy of Sciences of the USA 51:1207–1210.

MacArthur, R. H. 1972. Geographical ecology. Harper and Row, New York.

Merico, A., G. Brandt, S. L. Smith, and M. Oliver. 2014. Sustaining diversity in trait-based models of phytoplankton communities. Frontiers in Ecology and Evolution 2:59.

Metz, J. A. J., R. M. Nisbet, and S. A. H. Geritz. 1992. How should we define "fitness" for general ecological scenarios? Trends in Ecology and Evolution 7:198–202.

Mirrahimi, S., and S. Gandon. 2020. Evolution of specialization in heterogeneous environments: equilibrium between selection, mutation and migration. Genetics 214:479–491.

Mouillot, D., S. Villéger, M. Scherer-Lorenzen, and N. W. Mason. 2011. Functional structure of biological communities predicts ecosystem multifunctionality. PLoS ONE 6:e17476.

Norberg, J., D. P. Swaney, J. Dushoff, J. Lin, R. Casagrandi, and S. A. Levin. 2001. Phenotypic diversity and ecosystem functioning in changing environments: a theoretical framework. Proceedings of the National Academy of Sciences of the USA 98:11376–11381.

Norberg, J., M. C. Urban, M. Vellend, C. A. Klausmeier, and N. Loeuille. 2012. Eco-evolutionary responses of biodiversity to climate change. Nature Climate Change 2:747–751.

Nordbotten, J. M., F. Bokma, J. S. Hermansen, and N. C. Stenseth. 2020. The dynamics of trait variance in multi-species communities. Royal Society Open Science 7:200321.

Paine, C. E. T., C. Baraloto, J. Chave, and B. Hérault. 2011. Functional traits of individual trees reveal ecological constraints on community assembly in tropical rain forests. Oikos 120:720–727.

Peeters, F., and D. Straile. 2018. Trait selection and co-existence of phytoplankton in partially mixed systems: trait based modelling and potential of an aggregated approach. PLoS ONE 13: e0194076.

Raffard, A., F. Santoul, J. Cucherousset, and S. Blanchet. 2019. The community and ecosystem consequences of intraspecific diversity: a meta-analysis. Biological Reviews 94:648–661.

Ranjan, R., and C. A. Klausmeier. 2022. How the resource supply distribution structures competitive communities. Journal of Theoretical Biology 538:111054.

Rueffler, C., T. J. Van Dooren, O. Leimar, and P. A. Abrams. 2006. Disruptive selection and then what? Trends in Ecology and Evolution 21:238–245.

Sasaki, A., and U. Dieckmann. 2011. Oligomorphic dynamics for analyzing the quantitative genetics of adaptive speciation. Journal of Mathematical Biology 63:601–635.

Savage, V. M., C. T. Webb, and J. Norberg. 2007. A general multi-trait-based framework for studying the effects of biodiversity on ecosystem functioning. Journal of Theoretical Biology 247:213–229.

Schreiber, S. J., R. Bürger, and D. I. Bolnick. 2011. The community effects of phenotypic and genetic variation within a predator population. Ecology 92:1582–1593.

Siefert, A., C. Violle, L. Chalmandrier, C. H. Albert, A. Taudiere, A. Fajardo, L. W. Aarssen, et al. 2015. A global meta-analysis of the relative extent of intraspecific trait variation in plant communities. Ecology Letters 18:1406–1419.

Slatkin, M. 1980. Ecological character displacement. Ecology 61: 163–177.

Tirok, K., B. Bauer, K. Wirtz, and U. Gaedke. 2011. Predator-prey dynamics driven by feedback between functionally diverse trophic levels. PLoS ONE 6:e27357.

Troost, T. A., B. W. Kooi, and S. A. L. M. Kooijman. 2005. Ecological specialization of mixotrophic plankton in a mixed water column. American Naturalist 166:E45–E61.

Turcotte, M. M., and J. M. Levine. 2016. Phenotypic plasticity and species coexistence. Trends in Ecology and Evolution 31:803–813.

Turelli, M., and N. H. Barton. 1994. Genetic and statistical analyses of strong selection on polygenic traits: what, me normal? Genetics 138:913–941.

Umaña, M. N., and N. G. Swenson. 2019. Does trait variation within broadly distributed species mirror patterns across species? a case study in Puerto Rico. Ecology 100:e02745.

Uriarte, M., and D. Menge. 2018. Variation between individuals fosters regional species coexistence. Ecology Letters 21:1496–1504.

Violle, C., B. J. Enquist, B. J. McGill, L. Jiang, C. H. Albert, C. Hulshof, V. Jung, and J. Messier. 2012. The return of the variance: intraspecific variability in community ecology. Trends in Ecology and Evolution 27:244–252.

Volterra, V. 1928. Variations and fluctuations of the number of individuals in animal species living together. ICES Journal of Marine Science 3:3–51.

Westerband, A. C., J. L. Funk, and K. E. Barton. 2021. Intraspecific trait variation in plants: a renewed focus on its role in ecological processes. Annals of Botany 127:397–410.

Wickman, J., S. Diehl, B. Blasius, C. A. Klausmeier, A. Ryabov, and Å. Brännström. 2017. Determining selection across heterogeneous landscapes: a perturbation-based method and its application to modeling evolution in space. American Naturalist 189:381–395.

Wickman, J., S. Diehl, and Å. Brännström. 2019. Evolution of resource specialisation in competitive metacommunities. Ecology Letters 22:1746–1756.

Wickman, J., T. Koffel, and C. A. Klausmeier. 2022. Code from: A theoretical framework for trait-based eco-evolutionary dynamics: population structure, intraspecific variation, and community assembly. American Naturalist, Dryad Digital Repository, https://doi.org/10.5061/dryad.sqv9s4n72.

Wirtz, K.-W., and B. Eckhardt. 1996. Effective variables in ecosystem models with an application to phytoplankton succession. Ecological Modelling 92:33–53.

Xavier Jordani, M., N. Mouquet, L. Casatti, M. Menin, D. de Cerqueira Rossa-Feres, and C. H. Albert. 2019. Intraspecific and interspecific trait variability in tadpole meta-communities from the Brazilian Atlantic rainforest. Ecology and Evolution 9:4025–4037.

References Cited Only in the Online Enhancements

Bezanson, J., A. Edelman, S. Karpinski, and V. B. Shah. 2017. Julia: a fresh approach to numerical computing. SIAM Review 59:65–98.

Caswell, H. 2001. Matrix population models. 2nd ed. Sinauer, Sunderland, MA.

Chase, J. M., and M. A. Leibold. 2003. Ecological niches. University of Chicago Press, Chicago.

De Roos, A., T. Schellekens, T. Kooten, K. Wolfshaar, D. Claessen, and L. Persson. 2007. Food-dependent growth leads to overcompensation in stage-specific biomass when mortality increases: the influence of maturation versus reproduction regulation. American Naturalist 170:E59–E76.

Geritz, S. A. H., E. van der Meijden, and J. A. J. Metz. 1999. Evolutionary dynamics of seed size and seedling competitive ability. Theoretical Population Biology 55:324–343.

Koffel, T., T. Daufresne, and C. A. Klausmeier. 2021. From competition to facilitation and mutualism: a general theory of the niche. Ecological Monographs 91:e01458.

Owen, D. B. 1980. A table of normal integrals. Communications in Statistics—Simulation and Computation 9:389–419.

Rackauckas, C., and Q. Nie. 2017. Differentialequations.jl—a performant and feature-rich ecosystem for solving differential equations in Julia. Journal of Open Research Software 5:15.

Tilman, D. 1982. Resource competition and community structure. Monographs in Population Biology. Princeton University Press, Princeton, NJ.

Triantafyllopoulos, K. 2002. Moments and cumulants of the multivariate real and complex Gaussian distributions. Department of Mathematics, University of Bristol.

Associate Editor: Michael H. Cortez
Editor: Erol Akçay