

The Ecological Dynamics of Natural Selection: Traits and the Coevolution of Community Structure*

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ABSTRACT: Natural selection has both genetic and ecological dynamics. The fitnesses of individuals change with their ecological context, and so the form and strength of selective agents change with abiotic factors and the phenotypes and abundances of interacting species. I use standard models of consumer-resource interactions to explore the ecological dynamics of natural selection and how various trait types influence these dynamics and the resulting structure of a community of coevolving species. Evolutionary optima favored by natural selection depend critically on the abundances of interacting species, and the traits of species can undergo dynamic cycling in limited areas of parameter space. The ecological dynamics of natural selection can also drive shifts from one adaptive peak to another, and these ecologically driven adaptive peak shifts are fundamental to the dynamics of niche differentiation. Moreover, this ecological differentiation is fostered in more productive and more benign environments where species interactions are stronger and where the selection gradients generated by species interactions are stronger. Finally, community structure resulting from coevolution depends fundamentally on the types of traits that underlie species interactions. The ecological dynamics of the process cannot be simplified, neglected, or ignored if we are to build a predictive theory of natural selection.

Keywords: abundance dynamics, natural selection, niche differentiation, peak shift, trait cycling, trait dynamics, trait types.

Fitness is fundamentally an ecological quantity: an individual's fitness depends on how its phenotype translates the ecological conditions it experiences into survival, growth, and reproduction. Our understanding of how ecological processes shape species distributions, population dynamics, and community structure are built on the foundation that the fitnesses of individuals change with ecological context. Because the average fitness of all individuals in the population defines its per capita growth rate (e.g., Charlesworth

1994; Lande 2007), we typically discuss fitness changes in these contexts in the language of population growth. Hutchinson's (1958) niche is a concept of how per capita population growth rate (i.e., average fitness) changes with abiotic conditions across the landscape. Logistic population growth results from a declining per capita population growth rate with an increase in a species' own abundance (Verhulst 1838; Pearl and Reed 1920). Per capita growth rate also changes with the abundances of all the other species with which it interacts, and so whether species can coexist depends on the fitness effects of one on another (e.g., Volterra 1926; Lotka 1932a, 1932b; MacArthur 1972; May 1973; Holt 1977; Tilman 1982; Holt et al. 1994; Leibold 1996; Holt and Polis 1997; Chesson 2000).

To create a conceptual image that encompasses all of these aspects of population and community ecology, one can easily imagine expanding Hutchinson's (1958) hypervolume representation of a species' niche to describe an average fitness surface associated with axes quantifying abiotic environmental factors (as in his original description) and the abundances of all the species with which it interacts, including its own abundance. The topography of this fitness surface describes where this species can live, how its own abundance will change, and under what conditions it is capable of coexisting with the other species.

However, we know that this representation is incomplete, because the fitness of an individual also depends on both its own phenotype and the phenotypes of all its interaction partners. Every organism must secure resources, and many of those resources are other species that must be captured and subdued: a cheetah will starve if all of its prey can run faster than it can. Most organisms are also prey to others: the gazelle must run faster than the cheetahs to survive. Many organisms must also find mutualist partners: the shape of an orchid's flower will determine how successful visiting bees are at transferring pollen. Defensive traits must also be deployed to combat disease organisms and parasites. Therefore, this multidimensional fitness surface for a species must also be associated with axes

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describing its own traits as well as the traits of all the species with which it interacts. Were we to consider the relationship of fitness to only the trait axes of this species, Simpson's (1944) depiction of a dynamical fitness landscape emerges.

From this, it should be immediately apparent that natural selection must have strong ecological dynamics defined by the community of interacting species: the fitness surface against which a population evolves must change as the abundances and traits of itself and the other species that influence its fitness change. However, most inquiries of natural selection remove these ecological dynamics by assigning fixed fitness values to phenotypes and genotypes in order to focus on the genetic dynamics of the process, which can be quite complicated (e.g., Crow and Kimura 1970; Nagylaki 1992). We do this because we insidiously compartmentalize the trait dynamics of natural selection and the abundance dynamics of species interactions into separate realms. Evolution is by definition a change in the genetic composition of a population, and so inquiries naturally gravitate to the genetic dynamics of the process and ignore the determinants of fitness. Likewise, population dynamics are by definition a change in the abundance of a species, and so inquiries naturally gravitate away from the influences of traits or genes. Even our language and symbology blur the connections between abundance and trait dynamics: when considering trait dynamics, we discuss average fitness directly (e.g., $\ln(\bar{W})$), but when considering abundance dynamics, we discuss per capita population growth rate (e.g., dN/Ndt). However, dN/Ndt and $\ln(\bar{W})$ are the same quantity (e.g., Charlesworth 1994; Lande 2007), and ecologists and evolutionary biologists study different perspectives on the same whole.

As a highly simplified conception of this idea, consider the average fitness surface for a species depicted in figure 1C. Because I am limited to just three dimensions, I can show only the abundance and one trait axis for this species (in fact, multiple abundance axes would also be necessary if this species had a complex life cycle; Caswell 2001). The axes describing abiotic environmental factors and the traits and abundances of other interacting species are not illustrated, but I hope the reader can imagine them. At any instant in time, this community is represented as a point in the trait-abundance axis system, and the average fitness of this species is the height of the fitness surface above that point. Each species in the community will have a different fitness surface associated with the same axis system. The dynamics of natural selection at this instant are influenced by processes defining the shape of the fitness surface at its current abundance and the current traits and abundances for the other species. For example, if the current abundance is 50, imagine slicing this fitness surface at the abundance value of 50 with a plane that is parallel to the trait axis; this plane is also positioned at the current values on all the other axes that are not shown. The intersection of the fit-

ness surface with this slicing plane is the adaptive landscape that influences the evolution of this species at this instant (fig. 1A). The shape of this intersection will change as this slicing plane is moved to other positions on the various axes, and so the speed and trajectory of trait evolution as well as the trait value that natural selection favors will change. Likewise, the abundance dynamics at this instant are influenced by the shape of the relationship between per capita population growth rate (i.e., average fitness) and abundance. If the current trait mean is 10, imagine a slicing plane at a mean trait value of 10 for this species, at the current values on all the other axes that are not shown, and parallel to the abundance axis. The intersection of the fitness surface with this slicing plane defines abundance dynamics at this instant (fig. 1B). As the trait distribution in this population and the traits and abundances of the other species change (i.e., this slicing plane slides along the other axes), the per capita population growth rate for a given abundance and the equilibrium population size (i.e., the abundance at which $dN/Ndt = 0$) will change.

Understanding the drivers of fitness relationships in this way identifies the fundamental coupling between abundance and trait dynamics that cannot be severed. We have a long history of predicting the traits that should be favored by natural selection, but often these predictions are free of the dynamics of natural selection (e.g., optimization approaches; Maynard Smith 1978; Charlesworth 1990). However, where natural selection might move a population may not be apparent from the current fitness relationships, and whether any particular evolutionary outcome is reachable may depend on the abundance and trait responses of other species. Exploring the possible contours of the ecological dynamics of natural selection will also make the study of natural selection in the wild a more predictive endeavor, which may in turn generate a conceptually richer set of predictions about the processes structuring communities. Given that empirical studies of natural selection in the field provide only snapshots of these dynamics (e.g., quantifying the shape of the fitness surface at one instant in time; Lande and Arnold 1983; Arnold and Wade 1984; Kingsolver et al. 2001; Siepielski et al. 2009), theoretical studies of the ecological dynamics of natural selection are our best guides for how to combine these snapshots into a motion picture of evolution by natural selection.

In this paper, I explore major features of the ecological dynamics of natural selection in biological communities. In the first section, I operationalize this conceptual framework (fig. 1) using classic abundance dynamics models of species interactions coupled with classic trait dynamics models of quantitative characters. These coupled models actually have a long history. I have tried to analyze them here in ways that generate new predictions for empiricists studying natural selection in a single species or community structure in

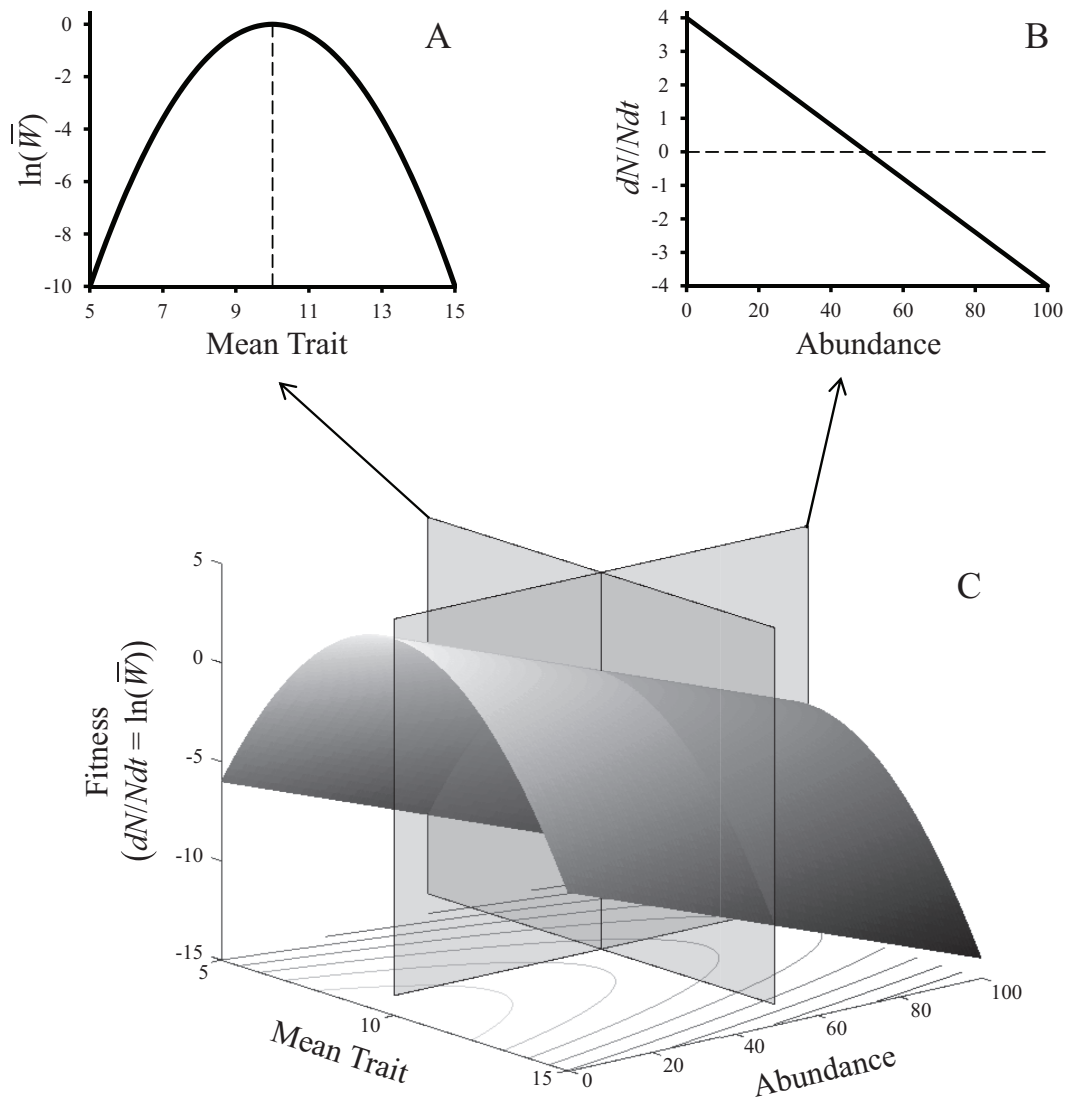


Figure 1: Average fitness surface for a hypothetical species and the more limited perspectives that evolutionists and ecologists take on this larger relationship. *C*, Overall fitness surface for this species. Because we are limited to three dimensions, the figure shows only the associated axes of one mean trait and the abundance axis for this species. In addition, this average fitness surface is associated with axes describing abiotic features of the environment and the abundances and traits of all the species with which this species interacts—these cannot be shown here but are part of the full conceptual system. Two slicing planes are shown through this fitness surface to represent the perspectives that evolutionists and ecologists take. *A*, Intersection of the overall average fitness surface with a slicing plane at an abundance value of $R = 50.0$ that runs parallel to the trait axis—the evolutionist’s perspective. *B*, Intersection of the overall average fitness function with a slicing plane at the trait value of $\bar{z}_k = 10.0$ that runs parallel to the abundance axis—the ecologist’s perspective.

multispecies assemblages. I use these models to first explore the coevolution of a single consumer species feeding on a single resource species to highlight major features of coupled abundance-trait dynamics in this simplest of systems. Situations where they come to a stable equilibrium and where their traits and abundances continuously cycle are used to highlight the important mechanistic features of their interaction. This exploration should provide additional insights

into how natural selection can be productively studied in the field. I also consider how the ultimate outcome of their coevolution depends on the ecological background (e.g., ecosystem productivity, stressors, habitat structural complexity) in which their interaction takes place. These results provide predictions for how the abundances and traits of species and the selection gradients acting on those traits may covary across populations distributed along environmental gradi-

ents. Finally, I explore the ecological differentiation of multiple species at multiple trophic levels in a food web. This analysis generates new predictions for how the ecological background and the types of traits underlying species interactions should foster or retard ecological differentiation at different trophic levels and how the structure of the resulting communities will differ along these environmental gradients and when different trait types are involved in species interactions. A fuller analysis addressing these issues and how natural selection shapes the coexistence of species in biological communities at both local and regional scales is forthcoming (McPeck 2017).

Population and Trait Dynamics

Models of abundance and trait dynamics that incorporate the density- and frequency-dependent dynamics of species interactions have a long history, and various approaches have been developed that make different assumptions about the genetic structure of populations. One approach generalizes Maynard Smith's (1983) game theoretic development of evolutionarily stable strategies to continuous time and a broader set of interacting types (e.g., Eshel 1983; Brown and Vincent 1987; Taylor 1989; Christiansen 1991; Cohen et al. 1999). A related approach termed adaptive dynamics assumes that a range of mutations continuously enter an asexual population at low frequencies (Metz et al. 1992, 1996, 1998; Dieckmann and Law 1996; Geritz et al. 1997). The third major approach elaborates the standard assumptions of quantitative genetics (Lande 1976) to model how the mean trait values of interacting species coevolve (e.g., Roughgarden 1976; Slatkin 1979a, 1979b, 1980; Lande 1982; Milligan 1985; Taper and Case 1985; Iwasa et al. 1991; Abrams et al. 1993b; Abrams 2000; Price and Kirkpatrick 2009; Schreiber et al. 2011). Much discussion has ensued about the relative benefits and realism of these various approaches (Taper and Case 1992; Abrams and Matsuda 1993; Abrams et al. 1993a; Taylor 1996; Abrams 2001a, 2001b; Cohen et al. 2001; Page and Nowak 2002; Waxman and Gavrillets 2005). Because it is most comparable with how natural selection is measured in the wild, I will employ the quantitative genetics approach in this analysis.

Many types of species interactions (e.g., resource competition, apparent competition, intraguild predation) are between various numbers of consumer and resource species. Many mutualisms are also consumer-resource interactions in which one species derives a net benefit from being consumed (Holland and DeAngelis 2010; Jones et al. 2012). Thus, I focus this analysis on simple consumer-resource interactions using a modified version of the classic Rosenzweig and MacArthur (1963) model as the framework. The basic model describes the abundance dynamics

of a resource species (R) that is fed upon by a consumer species (N):

$$\begin{aligned}\frac{dR}{dt} &= R \left(c - dR - \frac{aN}{1 + ahR} \right), \\ \frac{dN}{dt} &= N \left(\frac{baR}{1 + ahR} - f - gN \right).\end{aligned}\tag{1}$$

In this model, the abundance dynamics of each species are driven by a balance between per capita birth- and death rates. For the resource, its per capita birthrate ($c - dR$) is at a maximum defined by its intrinsic birthrate c when the resource is very rare ($R \approx 0$) and declines with its increasing abundance at a rate d (i.e., logistic growth). Likewise, the consumer's per capita death rate ($-(f + gN)$) is at a minimum defined by its intrinsic death rate f when the consumer is rare ($N \approx 0$) and increases with its increasing abundance at a rate g . Thus, both species may limit their own abundances through intraspecific density dependence, which can be important for multispecies coexistence at multiple trophic levels (McPeck 2012, 2014).

Their abundance dynamics are linked by the functional and numerical response terms describing predation by the consumer on the resource. The resource's per capita death rate is defined by Holling's (1959) saturating functional response ($aN/(1 + ahR)$), in which a is the attack coefficient for the rate at which a consumer kills resources, and h is the handling time. The consumer's per capita birthrate is the functional response multiplied by the conversion efficiency b , which defines the number of consumer offspring produced for each resource eaten. This model gives either a stable abundance point equilibrium or a stable abundance limit cycle depending on parameter values (Rosenzweig and MacArthur 1963; Rosenzweig 1969).

The parameters in this model are determined by the ecological milieu experienced by the populations. Specifically, the parameters encapsulate the effects of the various abiotic conditions and the abundances of all the other species not included in the model that are found at the location. In addition, the parameters are determined by the traits of all the interacting species. To keep things simple, I will assume that only one trait is ecologically important for each species. I assume that the resource's trait influences its intrinsic birthrate $c(z_R)$, the consumer's trait influences its intrinsic death rate $f(z_N)$, and the traits of both species influence the value of the attack coefficient $a(z_R, z_N)$; the conversion efficiency b , handling time h , and density-dependent rate parameters d and g will remain simply specified numbers. Consequently, the terms inside the outermost parentheses in equations (1) also specify the relationships between individual fitness and the phenotypic trait values of the interacting species:

$$\begin{aligned}\ln(W_R) &= c(z_R) - dR - \frac{a(z_R, z_N)N}{1 + a(z_R, z_N)hR}, \\ \ln(W_N) &= \frac{ba(z_R, z_N)R}{1 + a(z_R, z_N)hR} - f(z_N) - gN.\end{aligned}\quad (2)$$

Relationships such as equations (2) can be used to approximate the dynamics of the mean traits of these interacting species in a continuous-time representation of the standard breeder's equation formulation of natural selection, that is, the ecological dynamics of natural selection (Lande 1982; Iwasa et al. 1991; Abrams et al. 1993b). Under the standard assumptions of the genetics of quantitative traits (i.e., many loci of small and normally distributed effects), the change in the mean trait value of species i is approximated by

$$\frac{d\bar{z}_i}{dt} = V_{z_i} \left(\frac{\partial \ln(W_i)}{\partial z_i} \right) \Big|_{z_i = \bar{z}_i}, \quad (3)$$

where \bar{z}_i is the mean trait value in the population, V_{z_i} is the additive genetic variation in the trait, and the selection gradient acting on the trait (i.e., the partial derivative of individual fitness with respect to the trait) is evaluated at the mean trait value (Lande 1982; Iwasa et al. 1991; Abrams et al. 1993b). The appendix in Iwasa et al. (1991) provides an excellent explanation of the assumptions and derivations behind this approach. This framework can also be extended to incorporate multiple traits (Lande 1982; Iwasa et al. 1991) and complex life cycles (Barfield et al. 2011, 2012) in describing the evolution of each species, as well as be used to model phenotypic plasticity (Abrams 1992a, 1992b; Abrams et al. 1993b).

Applying this framework to equations (2) results in the following set of equations describing the trait dynamics of natural selection:

$$\begin{aligned}\frac{d\bar{z}_R}{dt} &= V_{z_R} \left(\frac{\partial(c(z_R) - dR)}{\partial z_R} \Big|_{z_R = \bar{z}_R} - \frac{\partial(a(z_R, z_N)N / (1 + a(\bar{z}_R, \bar{z}_N)hR))}{\partial z_R} \Big|_{z_R = \bar{z}_R} \right), \\ \frac{d\bar{z}_N}{dt} &= V_{z_N} \left(\frac{\partial(ba(z_R, z_N)R / (1 + a(\bar{z}_R, \bar{z}_N)hR))}{\partial z_N} \Big|_{z_N = \bar{z}_N} - \frac{\partial(f(z_N) + gN)}{\partial z_N} \Big|_{z_N = \bar{z}_N} \right).\end{aligned}\quad (4)$$

From this, overall selection can be decomposed into the constituents that describe how selection acts separately on the birth and death fitness components to determine the overall

trajectory of natural selection (Arnold and Wade 1984; Wade and Kalisz 1990; McPeck 1996). Note that the denominator of the functional response in the resource equation is evaluated at the mean trait value for the resource, because the satiation effect on the resource's death rate is assumed to be caused primarily by consumers being satiated by resources near their mean trait value (Abrams 2000). In contrast, the satiation effect in the consumer's numerical response evaluates satiation of that consumer individual's trait value (Abrams 2000). Local fitness maxima and minima on the overall fitness landscape that define the evolutionary equilibria for natural selection occur at mean trait values where these selection gradients exactly balance in each species (i.e., terms in the outermost braces of eqq. [4] sum to zero; Lande 1982; Iwasa et al. 1991; Abrams et al. 1993b). This formulation makes clear that what is favored overall by natural selection, even for very simple species interactions, is the mean trait value that optimizes the fitness consequences of different selective agents acting on various fitness components (e.g., Travis 1989).

Finally, the changes in abundances are approximated by assuming that the parameters in equations (1) are adequately represented by the parameter values associated with the mean trait values of the two species (i.e., expanding eqq. [1] with eqq. [2] and evaluating each at \bar{z}_i ; e.g., Abrams et al. 1993b; Abrams 2000). Expressed in their per capita forms, these are

$$\begin{aligned}\frac{dR}{Rdt} &= c(\bar{z}_R) - dR - \frac{a(\bar{z}_R, \bar{z}_N)N}{1 + a(\bar{z}_R, \bar{z}_N)hR}, \\ \frac{dN}{Ndt} &= \frac{ba(\bar{z}_R, \bar{z}_N)R}{1 + a(\bar{z}_R, \bar{z}_N)hR} - f(\bar{z}_N) - gN.\end{aligned}\quad (5)$$

Moreover, because these also express the average fitness of each species (i.e., $\ln(W_i)$), equations (5) define the corresponding average fitness surfaces for the two species that are associated with a four-dimensional axis system of R , N , \bar{z}_R , and \bar{z}_N (i.e., analogous to fig. 1C). Equations (4) define how each species moves along its trait axis, and equations (5) define how each species moves along its abundance axis. Abiotic environmental features are subsumed into the model parameters; that is, one can consider the model parameters to be values that transduce positions on the abiotic axes of the axis system in figure 1. Moreover, plotting each of equations (5) along only the trait axis of the corresponding species, given the current mean trait value of the other species and the current abundances of both, shows the current fitness landscapes defining their immediate evolutionary trajectories (i.e., the slicing plane intersection giving fig. 1A).

Different types of traits will have various functional relationships with various fitness components. One way to classify traits is based on how the selection gradient of a fitness component changes as the trait value is changed. A unidi-

rectional trait is one in which phenotypic change in one direction increases the fitness component over the entire range of the trait (following the terminology of Abrams 2000). Mathematically, this means that a unidirectional trait has $\partial(\text{fitness component})/\partial z_i > 0$ or $\partial(\text{fitness component})/\partial z_i < 0$ for all possible values of z_i , and so this fitness component would experience only directional selection. For example, spending greater amounts of time in its burrow should always increase the survival of a rabbit in the face of fox predation. Alternatively, a bidirectional trait has a reversal in the directionality of change in the fitness component of interest with trait change over different ranges of the phenotype; that is, $\partial(\text{fitness component})/\partial z_i > 0$ over some range of trait values, but $\partial(\text{fitness component})/\partial z_i < 0$ over another range (Abrams 2000). Therefore, a bidirectional trait must also have a fitness component maximum or minimum at some trait value where $\partial(\text{fitness component})/\partial z_i = 0$. A bidirectional trait will experience stabilizing or disruptive selection from that fitness component if the population's trait distribution includes the fitness component maximum or minimum, respectively, and it will experience directional selection if the population's trait distribution does not include the maximum or minimum. As an example of a bidirectional trait, consider a bird that feeds on the seeds of a plant that vary in size. Very small and very large seeds would have higher survival than seeds that closely match the sizes that are best manipulated by the bird's bill size.

Traits also differ in whether their contribution to determining a fitness component's value can be determined without reference to the trait value of another species. Some traits make independent contributions to the selection gradient on a fitness component. Increasing the time spent in its burrow will proportionally increase the rabbit's survival to a similar degree regardless of the fox's phenotype. This does not mean that the fox's phenotype has no influence on the rabbit's survival, but rather it only means that the contributions of the rabbit's and fox's phenotypes to the rabbit's survival can be conceptually and mathematically partitioned into independent components. In contrast, this conceptual and mathematical partitioning cannot be done for a dependent trait, because the fitness component contribution is a function of the difference or ratio of the phenotypes of the interacting species (when measured on appropriate scales). Again as an example, whether a seed of a particular size will have high or low survival depends on the size of the foraging bird's bill. Likewise, whether a particular running speed will confer high or low survival to a gazelle depends on how fast the cheetahs can run.

One can imagine a large constellation of trait effects on the fitness components of these species. Throughout this work, I will assume that the resource's birth fitness component and the consumer's death fitness component each have a bidirectional independent trait relationship. For the re-

source, I assume throughout that its intrinsic birthrate is maximized at a specified trait value \tilde{z}_R^c and declines as a quadratic function away from this intrinsic birth optimum as

$$c(z_R) = c_0(1 - \gamma(z_R - \tilde{z}_R^c)^2), \quad (6)$$

where c_0 is the maximum intrinsic birthrate, and γ scales the decline of the intrinsic birthrate away from \tilde{z}_R^c (i.e., the intrinsic selection gradient of the birth fitness component). Likewise, I assume that the consumer's intrinsic death rate is minimized at a specified trait value \tilde{z}_N^f and increases as a quadratic function away from this intrinsic death optimum according to

$$f(z_N) = f_0(1 + \theta(z_N - \tilde{z}_N^f)^2), \quad (7)$$

where f_0 is the minimum intrinsic death rate, and θ scales the increase in the intrinsic death rate away from \tilde{z}_N^f (i.e., the intrinsic selection gradient on the consumer's death fitness component).

Important differences among the various types of traits emerge when they underlie the interaction between species. In particular, some features of the dynamics of natural selection are different, and most importantly, fundamentally different community structures emerge as a result of differentiation through natural selection. Therefore, I will compare the outcomes when three different trait types underlie the attack coefficient defining the interaction between consumer and resource: a bidirectional dependent trait, a unidirectional dependent trait, and a unidirectional independent trait. All three of these trait types are commonly involved in how various consumers and resources interact with one another.

First, consider a bidirectional dependent trait underlying the attack coefficient. With this trait type, the attack coefficient is maximized when the traits of consumer and resource exactly match (when measured on appropriate scales), and the attack coefficient declines as the magnitude of the trait difference increases. Examples include the bill sizes of birds feeding on seeds of diverse sizes (Schluter and Grant 1984) and fish using gill rakers to filter zooplankton of various sizes (Schluter and McPhail 1993). I use a Gaussian function to model the attack coefficient as a function of the difference in the trait values between consumer and resource $\Delta = z_N - z_R$:

$$a(z_R, z_N) = a_0 e^{-(\Delta/\beta)^2}, \quad (8)$$

where a_0 is the maximum value when $\Delta = 0$, and β scales the rate of decrease in the attack coefficient away from $\Delta = 0$ in both directions (smaller values of β create a steeper decrease). The attack coefficient will be near its maximum possible value a_0 when the trait values of the two species are nearly identical and will be near zero if the resource's trait is very large or very small relative to the consumer's trait.

Other types of consumer-resource interactions are underlain by unidirectional dependent traits. These are inter-

actions where the fitness of each species increases in only one direction of trait change, but the fitness of each again depends on the difference in trait values ($\Delta = z_N - z_R$) between them. Escape speed is critical to many resources evading their consumers: if the resource can run or swim faster than its pursuing consumer, its chances of escape are high, but if the consumer can move faster than the resource, the resource will likely be caught (e.g., McPeck et al. 1996). Interactions in which the consumer is gape limited so that they cannot eat resource individuals above a certain size work in like fashion (e.g., Hambright 1994). Prey morphological defenses (e.g., spines, slime, armor, shells) also are unidirectional dependent trait systems underlying the attack coefficient (e.g., Havel and Dodson 1984). I model the attack coefficient underlain by such traits using a logistic function of the difference in trait values

$$a(z_R, z_N) = \frac{a_0}{1 + e^{-\alpha\Delta}}, \quad (9)$$

where a_0 is the asymptotic maximum, and α defines the steepness of transition from low to high values around $\Delta = 0$ (larger values of α create a steeper transition). The attack coefficient will be near zero if the resource's trait value is very large relative to the consumer's and will be near its maximum a_0 if the consumer's trait value is very large relative to the resource's.

Finally, many other traits independently influence the attack coefficient. For example, time spent active by the resource will change the attack coefficient independent of the effects of the consumer's trait. Likewise, time spent actively hunting resources by the consumer will have similar effects on the attack coefficient. For present purposes, I will focus on unidirectional independent traits such as resource and consumer activity that affect the conspicuousness and exposure of resources to consumers. The attack coefficient is zero if either z_R or z_N is zero, and the attack coefficient increases as either the resource or consumer trait increases. A function with these properties is the Michaelis-Menten equation (Michaelis and Menten 1913),

$$a(z_R, z_N) = a_0 \frac{z_R}{(\varepsilon_R + z_R)} \frac{z_N}{(\varepsilon_N + z_N)}, \quad (10)$$

where a_0 is again the asymptotic maximum, and $z_i/(\varepsilon_i + z_i)$ is the independent effect that the trait of species i has on the attack coefficient. The parameters ε_R and ε_N each scale the steepness of transition from zero to the asymptote for trait changes in the respective species, with smaller values resulting in a steeper transition.

To operationalize the models, equations (6)–(10) are substituted into the trait and abundance dynamic equations (4) and (5). The resulting sets of models that I explore here can be found in the appendix. An exhaustive exploration of trait type combinations and resulting parameter

spaces is beyond my scope here, and so I will explore only a small subset of trait combination types to highlight the main issues concerning the ecological dynamics of natural selection for various trait types and the consequences of those dynamics to the resulting community structure. For a fuller analysis, see McPeck (2017). The complexity of the system of equations also prohibits analytical solutions to the various models. Therefore, the following results are based on extensive explorations using numerical simulations. The Matlab (Mathworks, Natick, MA) code used for these simulations can be found in the supplementary material.¹

The Dynamics of Natural Selection

First, consider the factors driving the dynamics of a very simple scenario. The major features of this example are qualitatively the same with all three trait types underlying the attack coefficient, and so I will focus on the attack coefficient defined by bidirectional dependent traits. Imagine a bird species such as a Darwin's finch (the consumer) that feeds on the seeds of a plant (the resource), and the trait of the consumer (e.g., some aspect of bill morphology) influences its performance in feeding on seeds with various trait values (e.g., seed diameter). What are the ecological dynamics of coevolution as these two species adapt to one another? To begin, imagine that only the resource is present at a site, and it is adapted to its environment. This means that past selection has moved \bar{z}_R to the intrinsic birth optimum \tilde{z}_R^f (i.e., the trait value favored in the absence of the consumer), and the population is at its equilibrium abundance given this trait value mean in the population and no predation from the consumer.

Now allow the consumer to invade the site, starting at its intrinsic death optimum \tilde{z}_N^f as the trait mean and at a very low abundance (fig. 2; for a more dynamical visualization, see the animation of this figure; animations for figs. 2, 4–7 are available online). At the start, the consumer experiences strong selection to increase its trait value: the selection gradient on its birth fitness component is strongly positive because increasing its trait value will increase the realized attack coefficient on the resource, but the selection gradient on its death fitness component is near zero because it is near its death fitness optimum (iterations < 117; e.g., fig. 2C). Consequently, the consumer evolves to increase its trait value and increases in abundance from the start. However, the resource does not initially evolve at all, because the consumer is not abundant enough to inflict significant mortality on it. Consequently, the resource's death fitness component surface is nearly flat while the consumer is still rare, and so the resource's overall fitness surface nearly matches the

1. Code that appears in *The American Naturalist* is provided as a convenience to the readers. It has not necessarily been tested as part of the peer review.

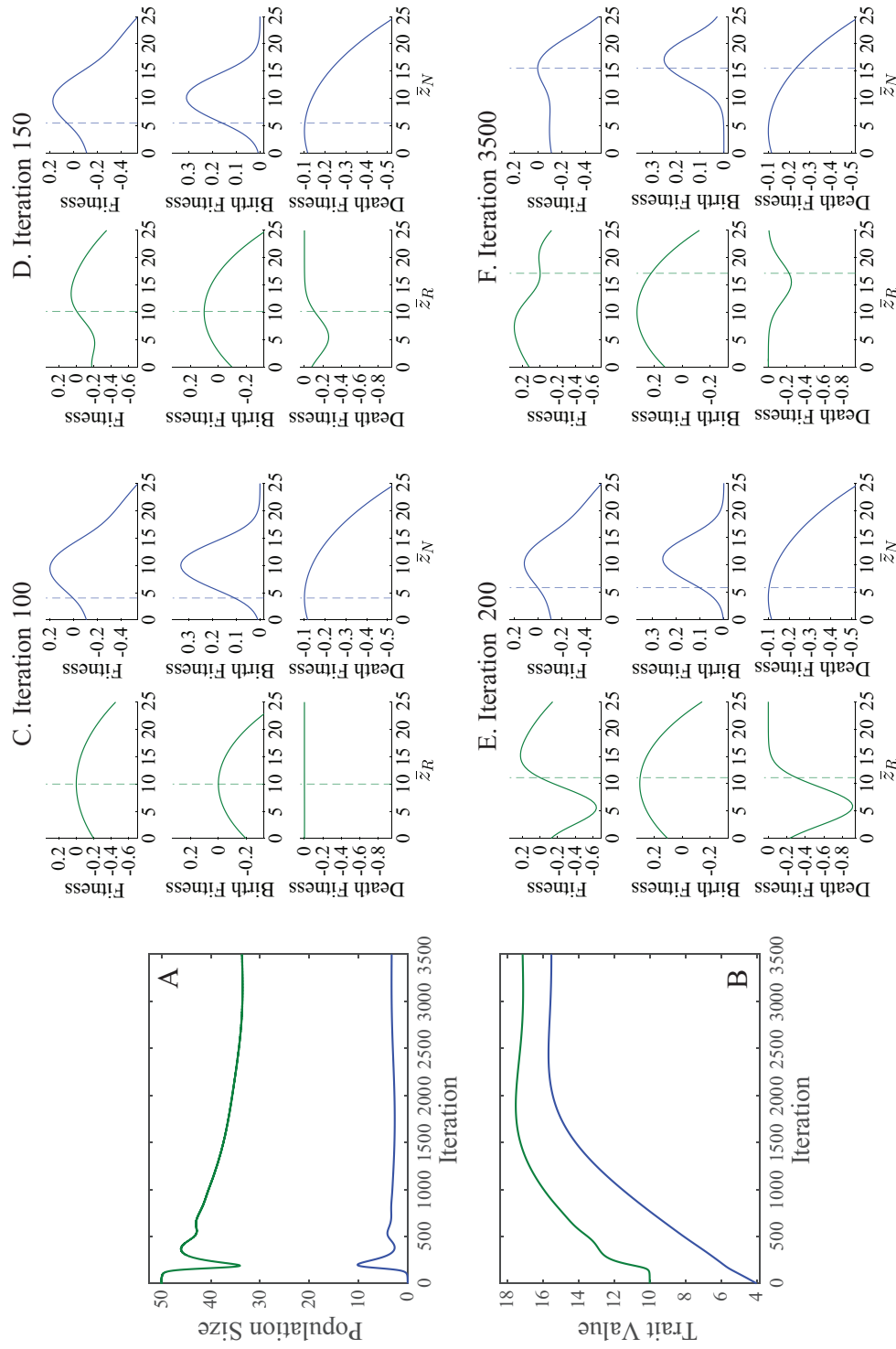


Figure 2: Abundance and trait dynamics of adaptation that occur when a consumer invades to feed on a resource and bidirectional dependent traits define the interaction between them. This simulation operationalizes equations (A1) in the appendix, with the following parameters: $c_0 = 1.0$, $d = 0.02$, $a_0 = 0.1$, $b = 0.1$, $h = 0.1$, $f_0 = 0.1$, $g = 0.0$, $\beta = 0.5$, $\gamma = 0.002$, $\theta = 0.01$, $\tilde{z}_R^c = 10.0$, $\tilde{z}_N^f = 4.0$, and $V_{z_N} = V_{z_R} = 0.2$. Initially, the resource species is at its demographic and evolutionary equilibrium in the absence of the consumer, with $\tilde{z}_R = 10.0$ and $R = 50.0$, and the consumer is at the trait value that minimizes its intrinsic death rate, $\tilde{z}_N = 4.0$, and very low abundance of $N = 0.01$. The population sizes (A) and mean trait values (B) change for the two species over the course of the simulation until they reach their joint abundance/trait equilibrium around iteration 3500. The trajectories for the resource are given in green and the consumer in blue. C-F, The various fitness surfaces for the two species at different iterations over the course of the simulation. The top graph in each column shows the overall fitness topography (i.e., plot of eq. [5] showing the slicing plane view of the fitness topography [i.e., as in fig. 1A]), the middle graph shows the topography for the birth fitness component (i.e., plotting only the birth component of eq. [5] against \tilde{z}), and the bottom shows the topography for the death fitness component (i.e., plotting only the death component of eq. [5] against \tilde{z}). The vertical dashed line in each identifies the location of the mean trait value in that iteration. The left column of graphs is for the resource species, and the right column is for the consumer species. An animation showing how these fitness topographies change smoothly over the entire course of the simulation is available online.

surface for its birth fitness component (iterations <117; e.g., fig. 2C). This highlights that the mere presence of the consumer does not favor the evolution of the resource away from the consumer; the consumer must be abundant enough to generate a substantial selection gradient on a fitness component of the resource to influence its overall fitness surface.

As the consumer continues to evolve a higher trait value and increases in abundance, it eventually starts imposing substantial mortality on the resource and generating a significant selection gradient on the resource's death fitness component (fig. 2D, iteration 150). At this point, the selection gradient on the resource's birth fitness component is zero because its phenotype still matches \bar{z}_R^c , but the selection gradient on its death fitness component is now positive. The change in the consumer's abundance and trait value has caused a substantial change in the fitness gradients experienced by the resource. As a result, the net selection gradient on the overall fitness surface is now also positive (fig. 2E), and the resource's trait mean shows a burst of rapid evolution away from the consumer (fig. 2B, iterations 152–246).

After this short evolutionary burst, their evolution slows, but the resource continues to evolve higher trait values and the consumer follows. As the resource evolves away from its intrinsic birth optimum, its abundance declines because of the resulting decrease in its realized intrinsic birthrate $c(\bar{z}_R)$, and its rate of evolution slows because the selection gradient on its birth fitness component becomes steeper. As the consumer evolves away from its intrinsic death optimum \bar{z}_N^d , its realized intrinsic death rate $f(\bar{z}_N)$ increases, but its abundance remains high because of its increased birthrate from adapting to the resource.

Eventually, the two species reach their joint demographic and evolutionary equilibrium. Their abundances equilibrate because their per capita birth- and death rates balance, and their trait values equilibrate because the selection gradients on their birth and death fitness components balance (fig. 2F, iteration 3500). The consumer is at a local adaptive peak on its overall fitness surface. Interestingly, the resource is at a local fitness minimum, which is a stable evolutionary equilibrium because of the dynamic nature of the underlying selection gradients. To understand why this fitness minimum is a stable equilibrium, we can perturb the resource's trait value away from this equilibrium and examine why the system returns to this point. If the resource's trait mean is lowered, the consumer's abundance immediately increases, which increases the selection gradient on the resource's death fitness component and alters its overall fitness surface to increase its trait value back to the evolutionary equilibrium. Conversely, if the resource's trait value is increased, the consumer's abundance declines, which decreases the selection gradient on the resource's death fitness component and thus changes its overall fitness surface to decrease its trait value back to the

equilibrium. This example forcefully illustrates that, because of density- and frequency-dependent selection, fitness minima and, thus, disruptive selection on the overall fitness surface are not necessarily unstable evolutionary equilibria (Abrams et al. 1993b). Although the population is experiencing disruptive selection, any evolutionary response by the population in any direction away from this equilibrium would alter the overall fitness surface to bring the population back to this equilibrium because of the abundance responses of other species (Abrams et al. 1993b). Moreover, the fitness surfaces experienced by species when they reach their joint demographic and evolutionary equilibrium are not those against which the species evolved to arrive at those positions (fig. 2C–2F; also see the animation).

Ecological Determinants of Traits Favored by Natural Selection

In addition to the transient evolutionary dynamics being strongly influenced by the ecological dynamics of the community, the ultimate outcome of coevolution between these two species also depends on the ecological context in which their interaction takes place and the underlying performance relationships between the traits and various fitness components. For example, these two species may interact with one another in various localities that differ in overall ecosystem productivity, which would cause the resource to have a different maximum birthrate (i.e., c_0 in eq. [6]) in each community. The conditions at different locations that cause stress in the consumer—or differences in the abundances of the consumer's other necessary resources that are not being modeled (e.g., water)—may generate different values of the consumer's minimum death rate (i.e., f_0 in eq. [7]). Likewise, the structural features of the environment (e.g., water turbidity for aquatic ecosystems, habitat structural complexity for all types of ecosystems) may also cause the maximum attack coefficient (i.e., a_0 in eq. [8]–[10]) to differ among communities in various locations. The parameters of these models reflect features of the environment (i.e., the positions on the abiotic axes of the conceptual framework as outlined earlier; fig. 1) and the nature of the interaction between the two species. In this section, I explore how varying these environmental features—the ecological background—through changes in the model parameters alter the trait values favored by natural selection. The qualitative features of the results I present here also do not depend on the type of traits underlying the attack coefficient, and so I continue in this section to show results only for attack coefficients defined by bidirectional dependent traits.

The productivity of a site will influence the birthrate of the basal resources in a community, with basal resources having higher maximum birthrates at sites with higher productivity. To see how productivity influences their coevolu-

tion, consider how the outcome of evolution between these two species differs among communities where the maximum resource birthrate c_0 differs (fig. 3A–3B). At very low values of c_0 ($c_0 < 2.8$ for the parameters considered in fig. 3A, 3B), the resource is not abundant enough to support a consumer population regardless of whether the consumer can adapt. Consequently, the resource trait value evolves to its intrinsic birth optimum ($\bar{z}_R^c = 12.0$ in fig. 3). If the resource's maximum intrinsic birthrate is high enough to support a consumer population, at higher values of c_0 , the resource eventually equilibrates at a trait value farther from its intrinsic birth optimum, and the consumer follows and so also equilibrates at a trait value farther from its intrinsic death optimum (fig. 3A).

The differences in evolutionary outcomes under different ecosystem productivities are again caused not by evolutionary features but rather by ecological features of the community. A higher resource intrinsic birthrate (larger c_0) permits the consumer to support a larger population (fig. 3B), which in turn generates a steeper selection gradient on the resource's death fitness component. Consequently, the selection gradients acting on the resource's two fitness components strike their balance farther from the resource's intrinsic birth optimum (\bar{z}_R^c). Moreover, higher resource productivity gives the consumer a higher realized birthrate, which allows it to support a population at a higher realized death rate, which also permits it to evolve farther from its intrinsic death optimum (\bar{z}_N^f). Thus, the selection gradients on both fitness components in both species are steeper at equilibrium with increasing environmental productivity, which suggests the general prediction that selection gradients on fitness components will be steeper in species up and down the food web in communities with higher basal productivity. (At very high c_0 values, the community enters an area of parameter space where trait cycling occurs; I will address these dynamics in the next section.)

Similar considerations emerge when we consider how these species evolve in various communities with environmental conditions that result in different consumer minimum death rates (f_0 ; fig. 3C, 3D). In an environmental setting that results in too high a minimum death rate (e.g., $f_0 > 0.39$ for the parameters considered in fig. 3C, 3D), again the consumer cannot support a population, and so the resource equilibrates at its intrinsic birth optimum (\bar{z}_R^c). In environmental settings with values below this point, lower values of f_0 cause both the resource and consumer to evolve higher trait values that are farther away from their respective intrinsic optimal phenotypes (\bar{z}_R^c and \bar{z}_N^f ; fig. 3C). A lower value of f_0 results in a lower realized death rate for the consumer, resulting in a larger consumer abundance (fig. 3D), which in turn creates a steeper selection gradient on the resource's death fitness component. Consequently, the selection gradients on both fitness components in both species are steeper

in what can be considered more benign environments for the consumer, another prediction from this analysis.

Environmental features that would affect the maximum value of the attack coefficient (a_0) will also influence the outcome of natural selection. In an environment where the maximum attack coefficient would be too low (e.g., $a_0 < 0.135$ for the parameters considered in fig. 3E, 3F), again the consumer cannot support a population even with evolution. In an environment with a_0 above this point, a higher maximum attack coefficient directly creates steeper selection gradients on both the resource's death fitness component and the consumer's birth fitness component, which causes both species to evolve trait values that are farther from their respective intrinsic birth and death optima (\bar{z}_R^c and \bar{z}_N^f ; fig. 3E). Thus, these results predict steeper selection gradients on fitness components of both species in communities where environmental conditions permit the consumer to catch the resource at a higher rate.

Not only does the environmental context in which the interaction takes place matter, but differences in the intrinsic features of a species interaction can also influence the outcome of evolution. For example, the relative strengths of the selection gradients acting on different fitness components will also shape the outcome of natural selection by how their relative strengths influence the topography of the overall fitness surface: components for which the fitness value changes faster for a given change in trait value will have greater influence on the shape of the overall fitness surface (Arnold and Wade 1984; Wade and Kalisz 1990; McPeck 1996). We can see this by varying the parameter scaling the rate at which the realized attack coefficient changes with a change in the difference between the bi-directional dependent traits of the two species (i.e., β in eq. [8]), while holding all the other parameters constant (fig. 3G, 3H). If the attack coefficient changes very slowly with a change in the difference in their trait values (i.e., large β), the consumer does not evolve very far from its intrinsic death optimum. Making this intrinsic gradient on the attack coefficient steeper (i.e., smaller values of β) causes the consumer to evolve to be closer in phenotype to the resource, which moves its trait value away from its intrinsic death optimum (fig. 3G) and thus causes the consumer's abundance to decrease (fig. 3H). Interestingly, in this case, changing β has very little effect on the trait value that evolves in the resource: the realized selection gradient on the resource's death fitness component changes little with a change in β because the increase in the attack coefficient gradient is offset by the decrease in consumer abundance. Altering the intrinsic gradients on the resource's realized birthrate (i.e., γ in eq. [6]) or the intrinsic gradient on the consumer's realized death rate (i.e., θ in eq. [7]) also changes the outcome of natural selection (fig. 3I–3L). These considerations illustrate the importance of quantifying the selection

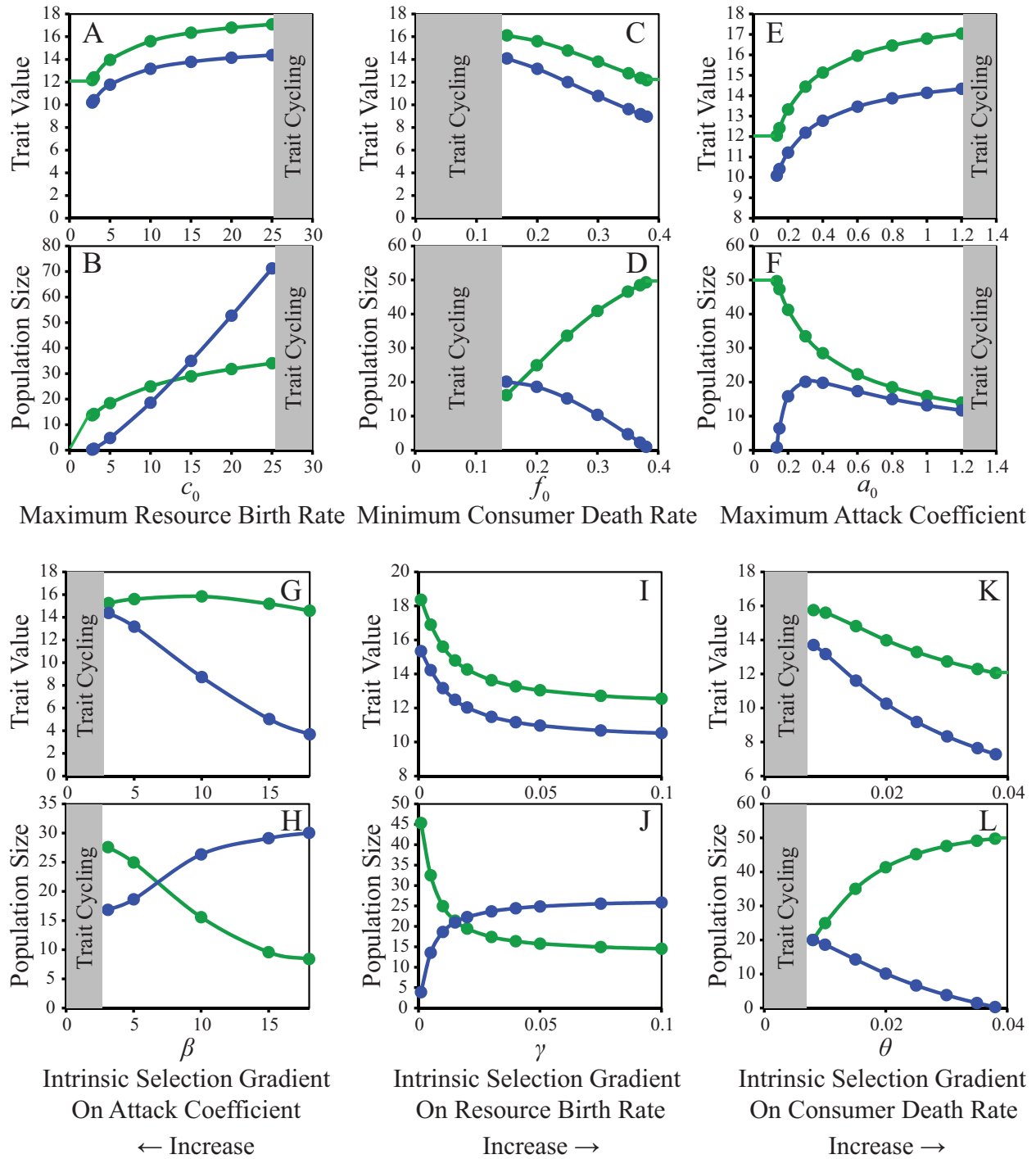


Figure 3: Evolutionary and demographic equilibria when a consumer and resource that interact through bidirectional dependent traits underlying the attack coefficient for various values of the maximum intrinsic birthrate of the resource (c_0 ; A, B), the minimum intrinsic death rate of the consumer (f_0 ; C, D), the maximum attack coefficient (a_0 ; E, F), the parameter scaling the intrinsic gradient of the attack coefficient (β ; G, H), the parameter scaling the intrinsic selection gradient of the resource birthrate (γ ; I, J), and the parameter scaling the intrinsic selection gradient of the consumer death rate (θ ; K, L). The equilibrium mean trait values for the resource (green) and consumer (blue) are given in the top panel of each pair, and the equilibrium abundances are given in the bottom panel of each pair. The gray boxes identify areas of parameter space where trait cycling occurs. Simulations of equations (A1) in the appendix with appropriate parameters were run until the abundances and trait values either came to a stable equilibrium or settled to a trait cycle. All parameters are as follows, except for the parameter being manipulated: $c_0 = 10.0$, $d = 0.2$, $a_0 = 0.5$, $b = 0.1$, $h = 0.1$, $f_0 = 0.2$, $g = 0.0$, $\beta = 5.0$, $\gamma = 0.01$, $\theta = 0.01$, $\tilde{z}_R^r = 12.0$, $\tilde{z}_N^f = 1.0$, and $V_{z_R} = V_{z_N} = 0.2$.

gradient strengths on various fitness components to understanding the form and result of natural selection overall.

In addition to the specific predictions outlined above, analyses like this should also inform how we quantify natural selection in the wild and interpret these measures (Endler 1986; Kingsolver et al. 2001). For example, one seeming paradox is that strong directional selection is commonly measured for traits with substantial additive genetic variation while measures of stabilizing selection in nature seem to be rare, but little evolutionary change occurs over multiple generations (Kingsolver et al. 2001; Merilä et al. 2001; Kingsolver and Diamond 2011). As the present analysis makes clear, stabilizing or disruptive selection would be quantified for overall fitness when a population is at its evolutionary equilibrium, but measures of selection on the underlying fitness components will typically be primarily directional. Instead of empty justifications for why some measure of a fitness component is a surrogate for overall fitness, we should embrace the fact that we mainly quantify phenotypic selection on fitness components (e.g., see Kingsolver et al. 2001). Obviously, populations of real species have many more than one ecologically important trait and have many simultaneously acting selective agents acting on numerous fitness components, which would make identifying the fitness balance nearly impossible to determine. However, exploring the interplay of selective agents on multiple traits and fitness components would more directly foster a much greater mechanistic and hypothesis-driven inquiry into the dynamics of natural selection (Wade and Kalisz 1990; McPeck 1996).

More mechanistic inquiries about the actions of various selective agents acting on different types of traits would also stimulate explicit testable hypotheses about the ecological and evolutionary factors generating spatial and temporal variation in phenotypic selection (Siepielski et al. 2009, 2011, 2013; Morrissey and Hadfield 2012). As this analysis makes clear, natural selection does not occur against a static fitness landscape that only changes with abiotic environmental conditions. The fitness landscape is itself dynamical and changes with intraspecific and interspecific abundances and as the trait distributions of other species change. How much of the spatial and temporal variation in selection gradients measured in natural populations can be explained by these biotic features of a species' ecological milieu?

Trait Cycling with Different Trait Types

Population abundance cycling is a well-understood dynamical phenomenon in which species' abundances undergo repeated large amplitude swings from low to high and back to low abundance because of limit cycles or chaos. Yoshida et al. (2003) have also shown that the characteristics of abundance cycles are different when interacting species are evolving. The coevolutionary models considered here also display in-

teresting dynamics in some limited areas of parameter space: the mean traits of the interacting species cycle, which in turn drives abundance cycling (e.g., Abrams and Matsuda 1997a, 1997b). Trait cycling occurs in more extreme areas of parameter space (e.g., high resource intrinsic birthrates, low consumer intrinsic death rates, high attack coefficients, and weak intrinsic fitness gradients on intrinsic fitness components but strong fitness gradients on fitness components influenced by species interactions; McPeck 2017). Therefore, trait cycling is likely rare in natural systems, but I want to consider trait cycling here for two reasons: the fundamental form of trait cycling differs when the traits underlying species interactions are of the different types, and considering their dynamics shows how a peak shift—the transition from one adaptive peak to another on a fitness topography—can be accomplished purely by the ecological dynamics of natural selection.

Figure 4 shows an example of trait cycling when bidirectional dependent traits underlie the attack coefficient (also see the animation of fig. 4). Here, the resource is undergoing repeated shifts between two adaptive peaks on its overall fitness surface, whereas the consumer's evolution is driven by chasing a single moving adaptive peak. Start at the point where the resource is at its highest trait value, and the consumer is evolving toward the resource (fig. 4B): the resource is at the pinnacle of one adaptive peak, and the consumer is evolving toward an adaptive peak that is near the resource's trait value (e.g., iteration 1833; fig. 4C). As the consumer continues to evolve toward the resource, the selection gradient on the resource's death fitness component declines, even though the death fitness component value increases. Consequently, the selection gradient on its birth fitness component is now relatively larger, the valley between the two adaptive peaks is now gone, and the resource actually begins to evolve toward the consumer. Evolving toward the consumer increases the resource's death rate from predation but further diminishes the strength of the selection gradient on the resource's death fitness component until the traits of the two species exactly match. At this point, only the resource's birth fitness component is experiencing directional selection (fig. 4D, iteration 1995). Once the resource's trait value passes the consumer's, the fitness valley between the two peaks reforms, and selection on both its fitness components drive the resource toward the lower fitness peak (fig. 4E, iteration 2099). Since the fitness peak for the consumer is always near the resource's trait value, the evolutionary trajectory of the consumer then reverses course to chase the resource to lower trait values, and the other half of the cycle begins. The same dynamical features happen in the other half of the cycle.

In this case, cycling takes the resource between trait extremes that give similar fitness outcomes of low birthrate and low death rate, but it must pass through a period of high birthrate and high death rate to move between these

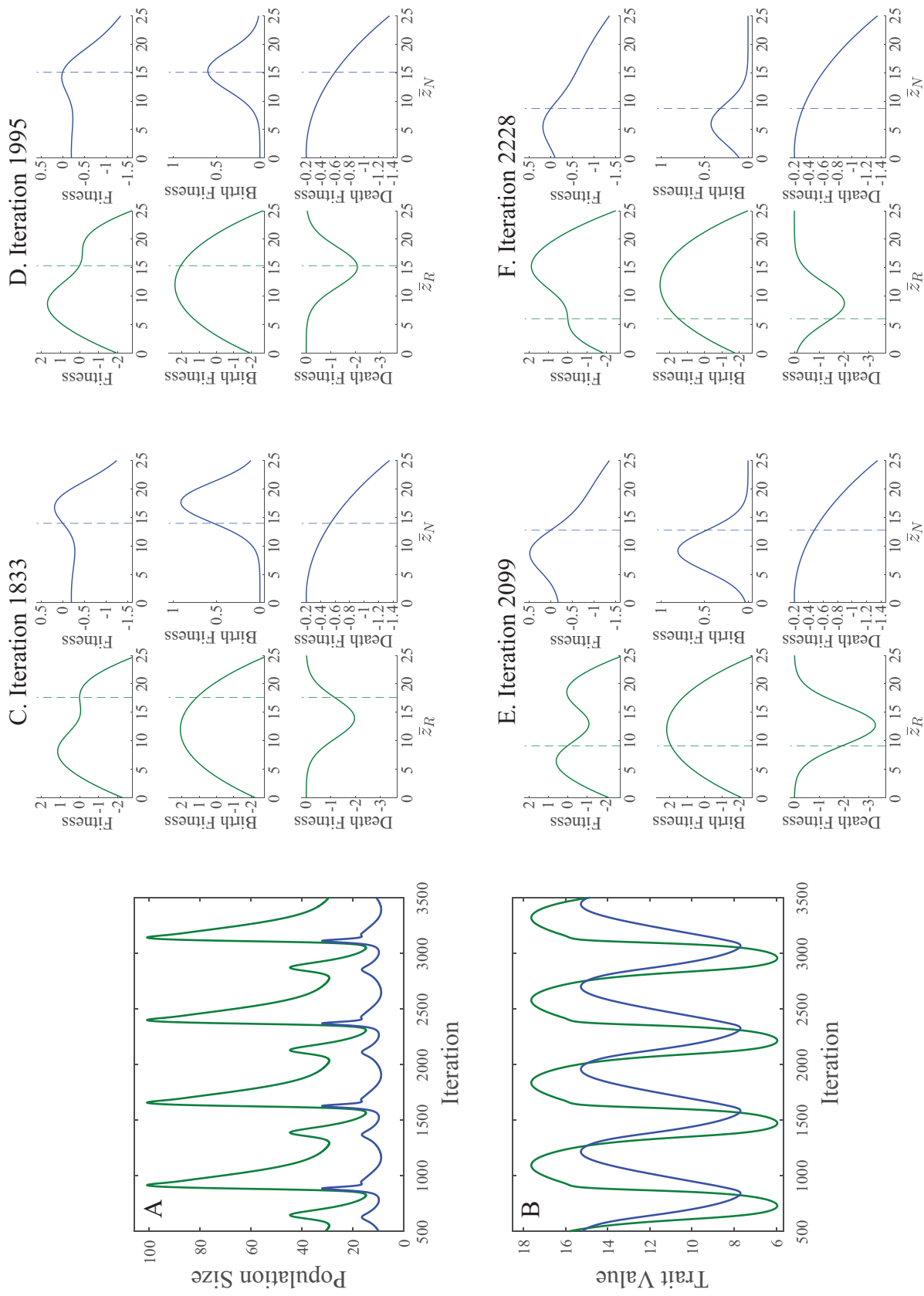


Figure 4: Trait cycling of a resource and consumer when bidirectional dependent traits underlie the attack coefficient. This simulation operationalizes equations (A1) in the appendix, with the following parameters: $c_0 = 3.0$, $d = 0.02$, $a_0 = 0.2$, $b = 0.1$, $h = 0.0$, $f_0 = 0.2$, $g = 0.0$, $\beta = 5.0$, $\gamma = 0.01$, $\theta = 0.01$, $\bar{z}_R^* = 12.0$, $\bar{z}_R^* = 1.0$, and $V_{\bar{z}_R} = V_{\bar{z}_N} = 0.2$. The panels are displayed as in figure 2, with C-F showing the overall and component fitness topographies for the two species at various iterations of the simulation. An animation showing how these fitness topographies change smoothly over the entire course of the simulation is available online.

extremes. The magnitudes of the selection gradients follow a countervailing trajectory: the selection gradients on both fitness components are steep near the trait value extremes, and the transit between the peaks (i.e., when the two species are most similar in their trait values) are periods in which the selection gradients on both are weak (fig. 4C–4F). Also, the magnitude of a fitness component is no reflection of the magnitude of the selection gradient acting on that fitness component. In this case, selection on both fitness components are strongest when the magnitudes of their values are relatively small, and each fitness component is at its maximum value at the point where no directional selection acts on it.

When the attack coefficient is underlain by unidirectional dependent traits (e.g., as when resource species evade capture by running or swimming; eq. [9]), trait cycling takes a different form (fig. 5; see also the animation). As with bidirectional dependent traits, cycling occurs because the resource is shifting between alternative peaks on its overall fitness surface, whereas the consumer chases a single moving peak. However, the fitness consequences of cycling are different. Cycling takes the resource from one fitness peak that is very near its intrinsic birth optimum, where it has its highest birthrate and highest death rate but the selection gradients are relatively weak on both fitness components (e.g., iteration 35843; fig. 5C), to the other fitness peak far away from its intrinsic birth optimum, where it has its lowest birthrate and lowest death rate but the selection gradients on both fitness components are steepest (e.g., iteration 41066; fig. 5D). Thus, in contrast to bidirectional dependent traits, cycling with unidirectional dependent traits defining the species interaction moves the resource between two alternative phenotypes that represent a trade-off of the fitness components (i.e., high birthrate and low survival rate [high death rate] versus low birthrate and high survival rate [low death rate]).

Trait cycling is quite different when the trait of each species has an independent effect on determining the interaction coefficient. Figure 6 shows trait cycling when the two species have unidirectional independent traits that define the attack coefficient (e.g., as with time spent active by each; eq. [10]; the animation of fig. 6 is available online). In this case, trait cycling only occurs in the resource, although the abundances of both species cycle in opposite phase from one another as a result (fig. 6; see also Yoshida et al. 2003). However, the resource's trait cycling occurs because of a simple reversal in the direction of selection and not peak shifts. These shifts in the direction of selection are driven largely by the changes in the abundances of the two species, and the resource cycles between extremes of low birth- and death rates to high birth- and death rates, which again is a trade-off of fitness components.

The underlying dynamics causing trait cycling are an object lesson in the ecological dynamics of natural selection.

The shape of the overall fitness surface is dynamical and, in this case, so dynamical as to drive peak shifts. Wright (1932) was the first to consider how a population might move from one adaptive peak to another in his development of the shifting balance process. His formulation of the problem, and most analyses that have followed, assumed unchanging fitnesses associated with genotypes or phenotypes and that stochastic factors (e.g., genetic drift or stochasticity in average fitness) caused peak shifts (e.g., Lande 1985, 1986; Rouhani and Barton 1987a, 1987b; Whitlock 1995, 1997; Whitlock et al. 1995). The examples considered here show how peak shifts can be accomplished purely by adaptive evolution driven by the ecological dynamics of natural selection. The basics of these peak shift dynamics will be critical to understanding the dynamics of species differentiation in the next section.

The Dynamics of Diversification and Community Structure

To now, I have considered only the coevolution of one consumer and one resource. Another essential function of natural selection in the development of community structure is determining the level of ecological differentiation among species that fill similar roles in the community. For example, if two nearly identical consumers feed on the resource species, would natural selection cause them to differentiate from one another? Or if two nearly identical resources were being fed upon by a single consumer, would natural selection cause them to differentiate?

Differentiation of similar species increases the functional diversity represented in a community. Moreover, the theory of community ecology is built on the assumption that species must be different to coexist with one another (e.g., MacArthur and Levins 1967; MacArthur 1972; Chesson 2000), with the presumption that natural selection should act to foster coexistence by driving this ecological differentiation (e.g., Brown and Wilson 1956; Hutchinson 1959; Connell 1980). Most of the early models of the ecological dynamics of natural selection examined whether natural selection would foster the differentiation of resource competitors (e.g., Roughgarden 1976; Slatkin 1980; Milligan 1985; Rummell and Roughgarden 1985; Taper and Case 1985; Abrams 1986, 1987a, 1987b; Doebeli 1996; Law et al. 1997; Kawecki and Abrams 1999). However, a frequently ignored but critical result of these theoretical studies is that ecological differentiation of similar species is not inevitable or even that likely (e.g., Slatkin 1980; Taper and Case 1985; Abrams 1990). Species differentiation may be fostered in some environmental conditions and retarded in others. In addition, the likelihood of differentiation and the structure of the resulting community may critically depend on the trait types involved in the species interaction. In this section, I explore

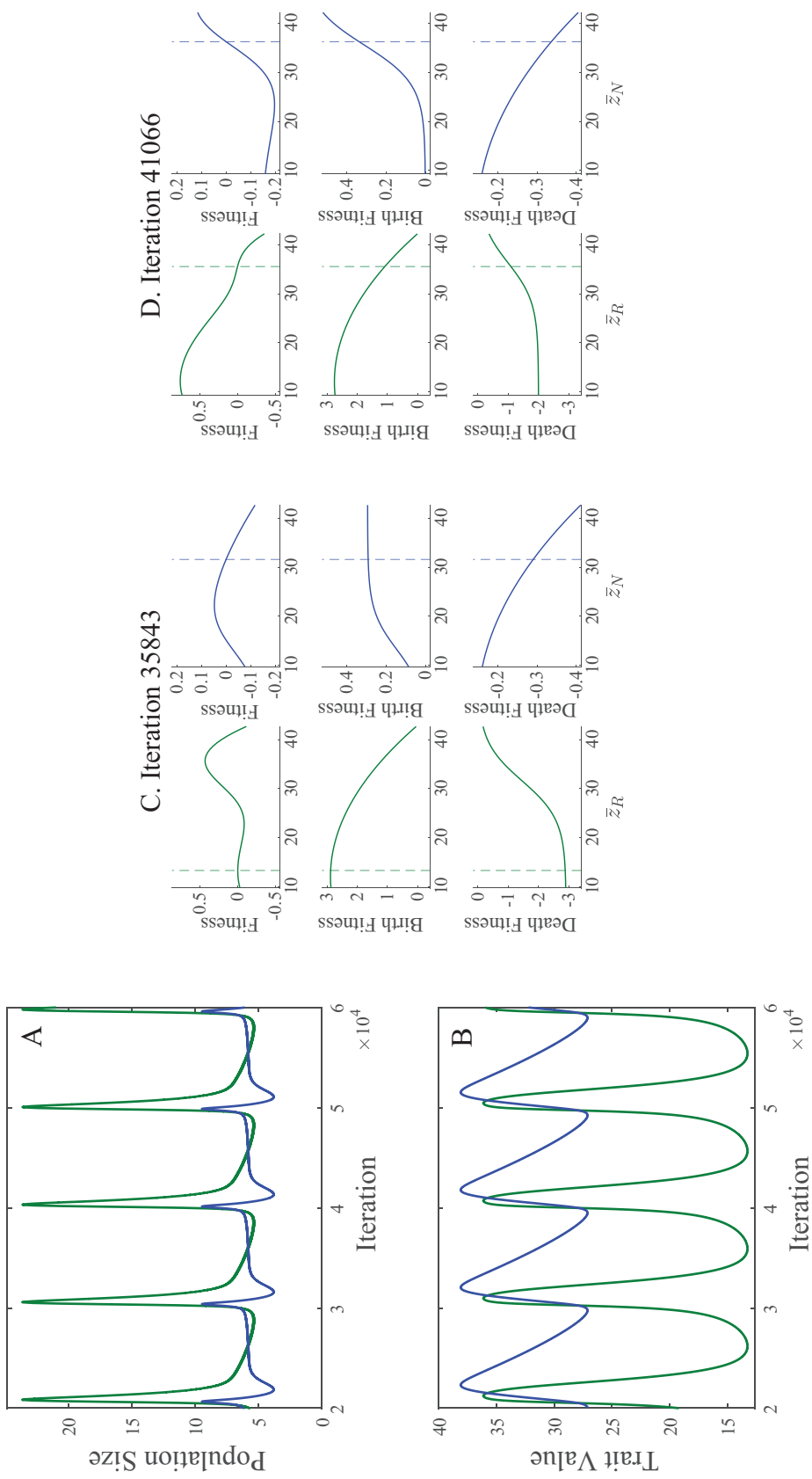


Figure 5: Trait cycling of a resource and consumer when unidirectional dependent traits underlie the attack coefficient. This simulation operationalizes equations (A2) in the appendix, with the following parameters: $c_0 = 3.0$, $d = 0.02$, $a_0 = 0.5$, $b = 0.1$, $h = 0.0$, $f_0 = 0.15$, $g = 0.0$, $\alpha = 0.25$, $\gamma = 0.001$, $\tilde{z}_R^f = 12.0$, $\tilde{z}_N^f = 1.0$, and $V_{z_s} = V_{z_c} = 0.2$. The panels are displayed as in figure 2, with C and D showing the overall and component fitness topographies for the two species at various iterations of the simulation. An animation showing how these fitness topographies change smoothly over the entire course of the simulation is available online.

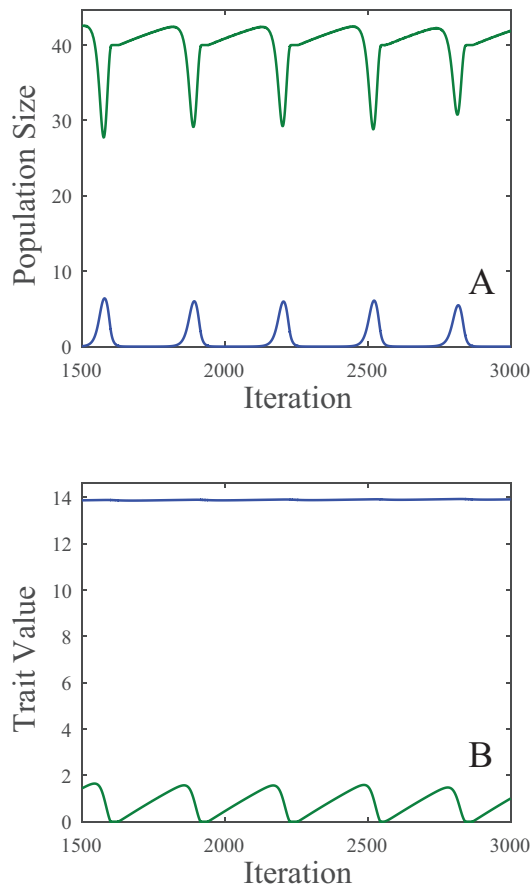


Figure 6: Trait cycling of a resource and consumer when unidirectional independent traits underlie the attack coefficient. This simulation operationalizes equations (A3) in the appendix, with the following parameters: $c_0 = 1.0$, $d = 0.02$, $a_0 = 3.5$, $b = 0.1$, $h = 0.3$, $f_0 = 0.1$, $g = 0.0$, $\varepsilon_R = 20.0$, $\varepsilon_N = 20.0$, $\gamma = 0.002$, $\theta = 0.001$, $\tilde{z}_k^f = 10.0$, $\tilde{z}_N^f = 1.0$, and $V_{z_R} = V_{z_N} = 0.2$. The panels are displayed as in figure 2. An animation showing how these fitness topographies change smoothly over the entire course of the simulation is available online.

the dynamics of ecological differentiation for species that have identical ecological capabilities, and I evaluate which ecological backgrounds may foster or retard their differentiation. The full set of equations used in this section are given in the appendix. A more expansive analysis in more complicated community structures (e.g., resource competition, apparent competition, diamond modules, omnivory and intraguild predation, and three-trophic levels) is presented in McPeck (2017), but the presentation here captures the essential elements fostering or retarding ecological differentiation.

To understand the dynamics of differentiation, first consider a simple community consisting of a single consumer feeding on two resources (i.e., apparent competition; fig. 7; see also Abrams 2000; Schreiber et al. 2011). The two resource species are identical in all parameters of the model,

and so they have identical ecological and evolutionary capabilities. This scenario can be interpreted as the ecological dynamics that act on two initially identical resource species that share a predator in a community of ecological equivalents (at a given trophic level) imagined by Hubbell (2001) or as the ecological dynamics that drives the sympatric ecological speciation of these two resource lineages (cf. Dieckmann and Doebeli 1999; Doebeli and Dieckmann 2000; Bolnick and Fitzpatrick 2007; van Doorn et al. 2009). I also consider this specific scenario to illustrate that ecological differentiation occurs as a result of all types of indirect species interactions (here apparent competition) and not just in response to resource competition (i.e., two consumers feeding on a single resource; Brown and Wilson 1956; Roughgarden 1976; Slatkin 1980; Milligan 1985; Taper and Case 1985; Brown and Vincent 1992). Again, bidirectional dependent traits underlie the attack coefficients in this example, but the dynamics of differentiation are similar with any of the trait types defining the attack coefficients. (See the animation of fig. 7.)

The two resource species start under the same adaptive peak far from their intrinsic birth optima and evolving away from the consumer, which is evolving toward them (fig. 7C, iteration 0). Just as with trait cycling, as the consumer approaches them in trait value, the selection gradients acting on the death fitness components of both resources decrease in magnitude so that the fitness valley separating the two fitness peaks disappears for both, and they both begin to evolve toward the consumer (starting at iteration 170 in fig. 7). The resource with the trait value nearer to the consumer matches and then passes the consumer's trait value first, again because of the increasing relative importance of selection on its birth fitness component (fig. 7D, iteration 454). Once the two resources straddle the consumer's phenotype, the consumer begins to evolve a lower trait value that balances its consumption of the two resources, and the fitness valley between the two adaptive peaks reforms on the fitness landscape of each resource species (e.g., iteration 520; fig. 7E). At this point, the two resources are now in the domains of attraction of different adaptive peaks. The community comes to an equilibrium with each resource occupying a different adaptive peak and the consumer at a stable fitness minimum between the two resources (fig. 7F, iteration 4000). Again, if the consumer is perturbed from this equilibrium trait value, the concomitant changes in the resources' abundances will alter the selection gradients acting on the consumer's birth fitness components (now the consumer has a separate birth fitness component for each resource: eqq. [A1] in the appendix) for the two resources so that overall selection returns the consumer to this stable equilibrium trait value.

Such ecological differentiation is not, however, inevitable. The ecological background in which the species interact influences whether differentiation will occur at a particular

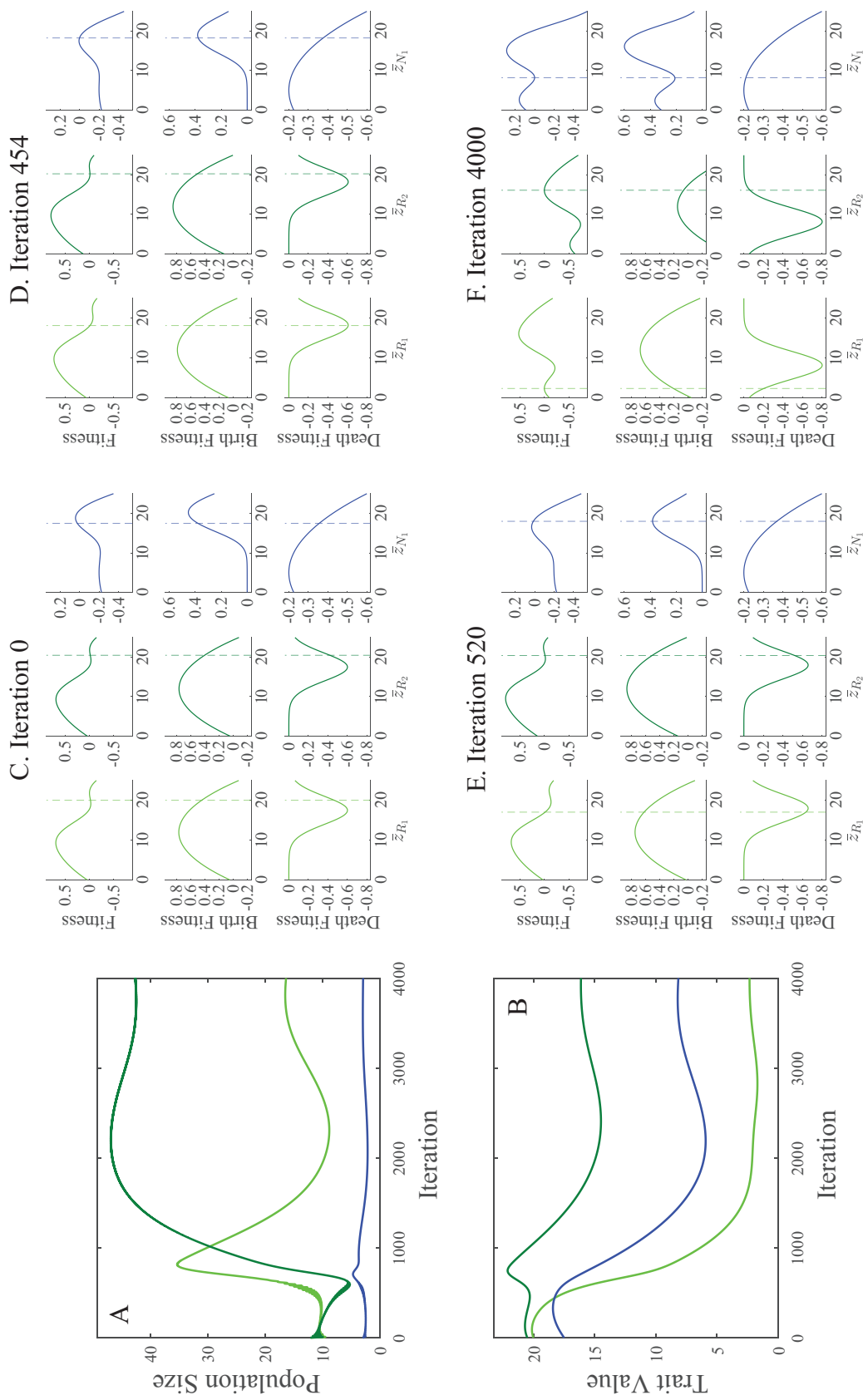


Figure 7: Two resource species differentiating from one another because they are being fed upon by a single consumer. Bidirectional dependent traits underlie the attack coefficients. This simulation operationalizes equations (A1) in the appendix, with the following parameters: $c_0 = 1.0$, $d = 0.02$, $a_0 = 3.5$, $b = 0.1$, $h = 0.10$, $f_0 = 0.2$, $g = 0.0$, $\beta = 5.0$, $\gamma = 0.005$, $\theta = 0.005$, $\bar{z}_k^b = 12.0$, $\bar{z}_k^f = 5.0$, and $V_{\kappa} = V_{\kappa} = 0.2$. The two resources are identified in the panels by different shades of green, and the consumer is in blue. Panels C–F are displayed as in figure 2, except that the left and middle columns in each panel present the fitness surfaces for the two resources. An animation showing how these fitness topographies change smoothly over the entire course of the simulation is available online.

trophic level. In what follows, I consider communities with two identically parameterized resources and two identically parameterized consumers (see appendix for the mathematical models used in simulations). Whether species differentiate and the outcome of that differentiation do not depend on initial conditions other than that species on the same trophic level cannot have identical initial trait values. I mainly present results using bidirectional dependent traits defining the attack coefficients, but I will note when other trait types generate different outcomes.

Productivity of the environment in which the community exists—interpreted as the maximum intrinsic birthrate of the resource c_0 —influences differentiation at both trophic levels. At the lowest values of c_0 that would support both consumers and resources ($0.05 < c_0 < 0.14$ in fig. 8A), species at neither trophic level differentiate from one another. A community in this range consists of two ecologically equivalent resource species with identical trait values and two ecologically equivalent consumer species with identical trait values (cf. Hubbell 2001). Under these conditions, the consumers cannot achieve a high enough abundance to generate two fitness peaks in the resources' fitness landscapes, and so the resources adapt to occupy the same adaptive peak. As a result, the two consumers also adapt to occupy the same adaptive peak that balances their feeding on the two identical resources with their death fitness component. If the resources' maximum intrinsic birthrates are somewhat higher ($0.14 < c_0 < 0.34$ in fig. 8A), the consumer abundances are high enough to drive the differentiation of the resources, but the consumers do not differentiate. This is because the consumers are at high enough abundance to generate two adaptive peaks in the resources' fitness surfaces, but the resources' traits are not far enough apart and their abundances are not high enough to generate two fitness peaks in the consumers' fitness surfaces. Finally, if their maximum intrinsic birthrates are high enough ($0.34 \leq c_0$ in fig. 8A), the traits of the differentiated resources evolve to be far enough apart (because of increased consumer abundances) to generate two fitness peaks in the consumers' fitness surfaces and thereby drive the differentiation of the consumers above them. Trait cycling of four differentiated species happens at very high values of c_0 . Thus, ecological differentiation is predicted to be more likely in higher productivity environments because differentiation at one trophic level is influenced by the abundances of species at other trophic levels. Additionally, because differentiation cascades up the food web, greater levels of productivity at the base of a food web are needed to drive differentiation at higher trophic levels.

Environmental conditions that generate different consumer intrinsic death rates (f_0) will also influence the likelihood of ecological differentiation (fig. 8B). In an environment in which the consumers' minimum intrinsic death rates are high, the consumers' abundances are not high enough to drive

the differentiation of the resources ($0.72 < f_0 < 1.2$ in fig. 8B; the consumers cannot support populations with $f_0 > 1.2$). In communities with intermediate values ($0.29 < f_0 < 0.72$), the consumers are abundant enough to drive the differentiation of the resources, but the consumers do not differentiate. Only when the consumers' intrinsic minimum death rate is relatively low (and so they can achieve higher abundances) will species at both trophic levels differentiate ($f_0 \leq 0.29$). Thus, ecological differentiation is expected to be more likely in environments that are more benign to species at higher trophic levels. A similar progression of differentiation at the two trophic levels also follows in communities in which the maximum attack coefficients are different, again because of the effects that the maximum attack coefficient has on the abundances of species at both trophic levels (fig. 8C).

The effects considered so far are mediated through changes in abundances. Differences in the underlying strengths of selection gradients acting on the various fitness components (e.g., the relative values of γ , θ , and β) will also influence whether differentiation occurs. If the selection gradients acting on fitness components not involved in the species interaction of either the resource (birth) or consumer (death) are relatively weak (i.e., small values of γ or θ , respectively), the selection gradients on their fitness components defined by the species interactions are more important to determining the shape of their overall fitness surfaces, and so species at both trophic levels differentiate (fig. 8D, 8E). However, if the intrinsic selection gradients on the fitness components not involved in the species interactions are steep relative to the underlying selection gradient on the attack coefficient, species at neither trophic level differentiate. At intermediate values for these, only the resources differentiate (fig. 8D, 8E).

The converse is true for fitness components involved in the species interactions. Higher values of the intrinsic gradients on the attack coefficients, which increase the selection gradients on the resources' death fitness components and the consumers' birth fitness components, foster ecological differentiation (fig. 8F). However, weak intrinsic gradients on the attack coefficient permit each species to adapt mainly by bettering its intrinsic needs without sacrificing too much in the species interaction, and so species at neither trophic level differentiate (fig. 8F). Thus, whether closely related and ecologically similar or identical species will differentiate from one another depends not only on the abundances of the interacting species but also on the fundamental mechanisms defining how the various fitness components change with trait change.

When differentiation of species at a particular trophic level occurs, the dynamics of natural selection driving the differentiation is the same when taxa have other trait types that define their interactions. In addition, differentiation is fostered in comparable areas of parameter space for all trait types. However, the ranges of parameter space are very

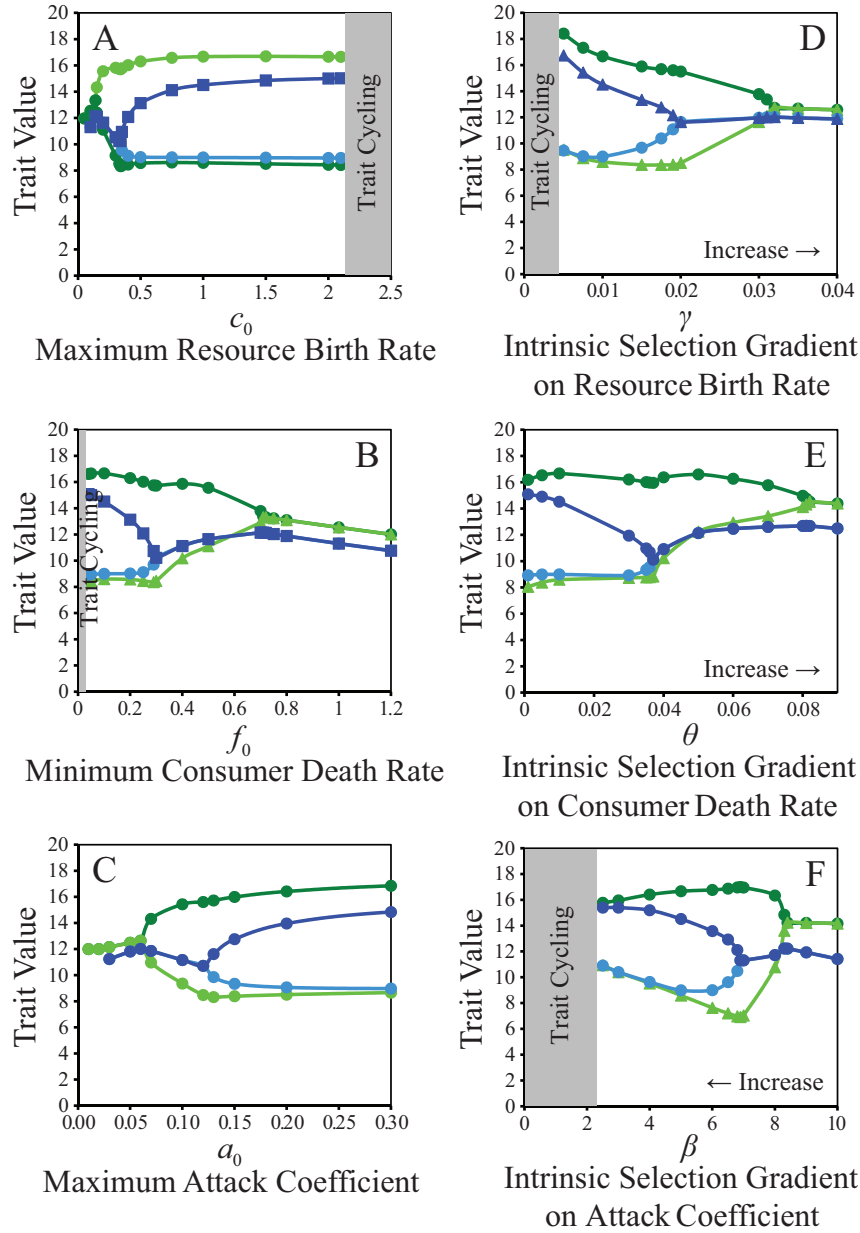


Figure 8: Evolutionary trait equilibria for two identically parameterized consumers feeding on two identically parameterized resources, and bidirectional dependent traits underlie the attack coefficients, for various values of the resource's maximum intrinsic birthrate (A), the consumer's minimum intrinsic death rate (B), the maximum attack coefficient (C), the parameter scaling the intrinsic selection gradient of the resource birthrate (D), the parameter scaling the intrinsic selection gradient of the consumer death rate (E), and the intrinsic gradient of the attack coefficients (F). The two resources are shown in different shades of green, and the two consumers are shown in different shades of blue. Gray boxes identify areas of parameter space where trait cycling occurs. Simulations of equations (A1) in the appendix with appropriate parameters were run until the abundances and trait values either came to a stable equilibrium or settled to a trait cycle. All parameters are as follows, except for the parameter being manipulated: $c_0 = 1.0$, $d = 0.02$, $a_0 = 0.25$, $b = 0.1$, $h = 0.10$, $f_0 = 0.1$, $g = 0.1$, $\beta = 5.0$, $\gamma = 0.01$, $\theta = 0.01$, $\tilde{z}_R^f = 12.0$, $\tilde{z}_N^f = 1.0$, and $V_{z_R} = V_{z_N} = 0.2$.

different where differentiation is fostered for the various trait types underlying the attack coefficients (McPeck 2017). Extensive explorations of parameter space with simulations indicate that differentiation occurs in somewhat smaller areas

of parameter space when unidirectional dependent traits (i.e., eq. [9]) define the attack coefficients than with bidirectional dependent traits (McPeck 2017). The pattern of differentiation still has comparable areas in which neither trophic level

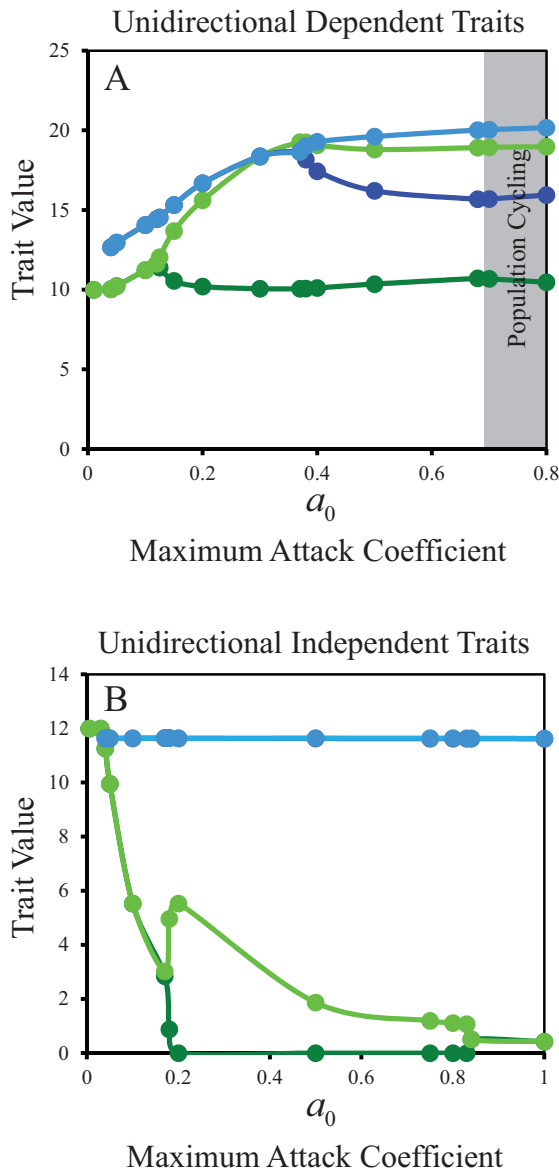


Figure 9: Evolutionary trait equilibria for two identical parameterized consumers feeding on two identical parameterized resources for various values of the maximum attack coefficient when unidirectional dependent traits (A) or unidirectional independent traits (B) underlie the attack coefficients. The two resources are shown in different shades of green, and the two consumers are shown in different shades of blue. Gray boxes identify areas of parameter space where trait cycling occurred. Simulations of equations (A2) and (A3) in the appendix with appropriate parameters were run until the abundances and trait values either came to a stable equilibrium or settled to a trait cycle. For unidirectional dependent traits (A), the parameters are $c_0 = 1.0$, $d = 0.02$, $a_0 = 0.5$, $b = 0.1$, $h = 0.1$, $f_0 = 0.15$, $g = 0.1$, $\alpha = 0.75$, $\gamma = 0.005$, $\theta = 0.005$, $\tilde{z}_R^c = 10.0$, $\tilde{z}_N^f = 1.0$, and $V_{z_R} = V_{z_N} = 0.2$. For unidirectional independent traits (B), the parameters are $c_0 = 1.0$, $d = 0.02$, $a_0 = 0.5$, $b = 0.1$, $h = 0.3$, $f_0 = 0.05$, $g = 0.1$, $\varepsilon_R = 15.0$, $\varepsilon_N = 15.0$, $\gamma = 0.003$, $\theta = 0.003$, $\tilde{z}_R^c = 12.0$, $\tilde{z}_N^f = 2.0$, and $V_{z_R} = V_{z_N} = 0.2$.

differentiates, only the resources differentiate, or both trophic levels differentiate (e.g., fig. 9A).

Ecological differentiation occurs over much smaller areas of parameter space when independent traits define the attack coefficient (McPeck 2017). For example, figure 9B presents a typical pattern for unidirectional independent traits (eq. [10]) defining the attack coefficients. First, I could find no conditions where differentiation of identical resource species would drive the differentiation of identical consumers, implying that differentiation at one trophic level will not drive the differentiation of species at another trophic level with independent traits. Moreover, differentiation only occurs when a resource can support a population with a trait value of zero (e.g., being completely invulnerable to predation when being completely inactive). Also, at high values of the resources' intrinsic birth rates, low values of the consumers' intrinsic death rates, and high values for the attack coefficients, the resources did not differentiate (e.g., as in fig. 9B): in this area of parameter space, simply being nearly invulnerable is the only viable strategy. Thus, unlike dependent traits, differentiation of the resources only occurs at intermediate values of these parameters.

Another important difference among the trait types is the structure of the resulting communities when bidirectional versus unidirectional traits define species interactions. With bidirectional traits defining species interactions, each consumer species imposes the greatest mortality on a different resource species (i.e., the resource species most similar to it in trait value; fig. 10B), which results in the differentiated consumers specializing in large measure on different resources. In contrast, when unidirectional traits define the attack coefficients, every consumer has the same hierarchy of interaction strengths with the resource species since the relative ranks of the resources are based on the relative ranks of the resources' trait values (fig. 10A). Thus, limiting similarity arguments about community structure (e.g., Hutchinson 1959; MacArthur and Levins 1967; Roughgarden 1974; Abrams and Rueffler 2009) only apply when species interactions are defined by bidirectional traits, whereas hierarchical and nested species interaction networks (e.g., Bascompte et al. 2003, 2006; Jordano et al. 2003; Vázquez and Simberloff 2003) result when unidirectional traits underlie species interactions.

These results about the drivers of ecological diversification suggest a number of testable predictions. For example, ecological diversification of closely related species should be more prevalent in more productive and more benign environments. In these types of habitats, species interactions should be more important to the fitness dynamics of each interacting species through increases in the abundances of species. One obvious relationship this suggests is the latitudinal diversity gradient in which species richness increases with decreasing latitude. One explanation that has been recently advanced for this pattern is that species interactions are stronger in the tropics than in polar or temperate re-

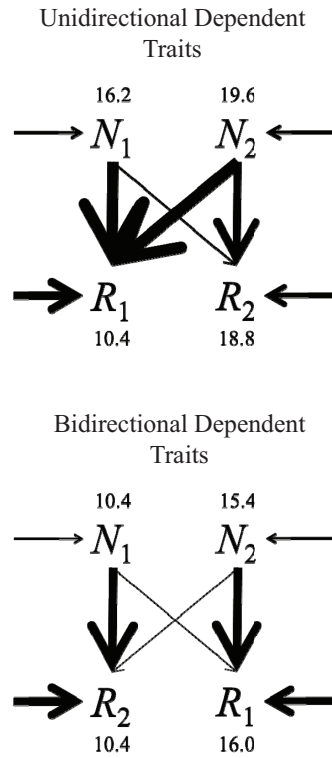


Figure 10: Strengths of interactions among consumers and resources that have both differentiated when the attack coefficients are underlain by unidirectional dependent traits (A) and bidirectional dependent traits (B). The numbers next to the species symbol is the mean trait value for that species at equilibrium. The size of the arrows pointing from a consumer to a resource is proportional to the magnitude of the realized attack coefficient for the interaction between these two species. The arrows pointing toward the consumers' identifiers are the magnitude of their realized intrinsic death rates ($f(\bar{z}_N)$), and the arrows pointing toward the resources' identifiers are the magnitudes of their realized intrinsic birthrates ($c(\bar{z}_R)$). For unidirectional dependent traits, the parameters are $c_0 = 1.0$, $d = 0.02$, $a_0 = 0.5$, $b = 0.1$, $h = 0.1$, $f_0 = 0.15$, $g = 0.1$, $\alpha = 0.75$, $\gamma = 0.005$, $\theta = 0.005$, $\bar{z}_R^c = 10.0$, $\bar{z}_N^f = 1.0$, and $V_{z_R} = V_{z_N} = 0.2$. For bidirectional dependent traits, the parameters are $c_0 = 1.0$, $d = 0.02$, $a_0 = 0.25$, $b = 0.1$, $h = 0.0$, $f_0 = 0.1$, $g = 0.01$, $\beta = 3.0$, $\gamma = 0.01$, $\theta = 0.01$, $\bar{z}_R^c = 12.0$, $\bar{z}_N^f = 1.0$, and $V_{z_R} = V_{z_N} = 0.2$.

gions (Schemske et al. 2009). The model results presented here provide a mechanistic basis for how the strength of species interactions may actually drive the fitness dynamics of natural selection to generate this pattern. One test of this prediction would be that selection gradients on fitness components associated with species interactions should be steeper with decreasing latitude.

These results also predict that ecological differentiation should be most prevalent in taxa where dependent traits and bidirectional traits define the mechanisms of their interactions with other species. Incidentally, many of our best-studied examples of ecological diversification are taxa with

bidirectional dependent traits defining their interactions with other species. Darwin's finches feeding on seeds of various sizes is an excellent example of such a differentiated taxon (Schluter and Grant 1984; Grant and Grant 2006). The morphological features of the bill define an optimal seed size on which a particular finch can feed: seeds are safer from a particular finch as their size becomes larger or smaller than this optimal size (Schluter and Grant 1984). Limb and body size matching to various branch diameters in Caribbean *Anolis* lizards also represents the result of ecological diversification based on bidirectional dependent traits (Schoener 1974; Losos 1990a, 1990b). Gill raker and body size differences between benthic and limnetic species of sticklebacks in some Vancouver Island lakes also resulted from the diversification of a taxon based on bidirectional dependent foraging traits (Schluter and McPhail 1993).

As an aside, it is also interesting to note that most lakes on Vancouver Island harbor only one stickleback species. Might the six lakes with two stickleback species be those with the most favorable environmental conditions for ecological differentiation (e.g., higher productivity and more benign conditions for sticklebacks to permit higher abundances, and environmental conditions such as less turbid waters that foster more intense species interactions)?

Because of these and other exemplars of ecological differentiation within a local community, I have always been puzzled by why the *Enallagma* damselflies are so ecologically similar. Five to 12 *Enallagma* species can be found in every lake in which fish are the top predators from the Gulf of Mexico to southern Canada (Johnson and Crowley 1980; Crowley and Johnson 1982; McPeck 1990b, 1998). All the species are extremely similar in ecological performance metrics (mortality rates due to fish predation, individual growth rates, adult fecundities) and in ecologically important phenotypes (antipredator behaviors, foraging rates, physiological stress responses to predators, digestive physiological capabilities, adult mating behavior; McPeck 1995, 1999; Stoks et al. 2003; Stoks and McPeck 2006). As expected based on their similar phenotypes, field experiments using two *Enallagma* species whose last common ancestor is the phylogenetic basal node of the entire genus (8–9 million years ago; Callahan and McPeck 2016) have also shown that these species are ecologically indistinguishable (Siepielski et al. 2010). As a result of 30 years of field and laboratory work, my conclusion is that 8–9 million years of lineage diversification to produce the 34 extant fish-lake *Enallagma* in North America was accomplished primarily by differentiation of mate recognition systems (McPeck et al. 2008, 2009, 2011), with little to no ecological diversification whatsoever either during or after speciation in this lake type.

I have always wondered why my friends and colleagues all got to work on ecologically diverse taxa, but this genus of damselfly I picked to study turned out to be so species

rich but so ecologically homogeneous in this habitat (i.e., Oh, woe is me!). This theoretical analysis has finally suggested a hypothesis for why these co-occurring *Enallagma* species have never differentiated. These species all avoid fish predators by being relatively inactive (McPeck 1990a; Stoks et al. 2003; Stoks and McPeck 2006)—a unidirectional independent trait. Being completely inactive is probably not an option for *Enallagma* larvae because they must move through the stems of macrophytes to forage for their own food. Thus, the antipredator strategy of fish-lake *Enallagma* is one that offers the least chance of species differentiating, based on the models presented here. Fish-lake *Enallagma* may occupy an area of parameter space in which selection on activity and other traits offers only one adaptive peak to all species.

Final Thoughts

In recent years, the realization that ecological and evolutionary processes do not have separate timescales has flourished. In fact, a number of new terms (e.g., ecoevolutionary, ecogenetic) have been coined to identify situations in which both abundance and trait dynamics can be perceived simultaneously (e.g., Fussmann et al. 2007; Kokko and López-Sepulcre 2007; Schoener 2011). While I understand the desire to create a more precise terminology, I think these terms may be counterproductive to our broader conceptual understanding. Ecology and evolution are simultaneously essential to understanding the place of a species in a community and, in fact, the structure of entire communities, even when abundances and traits are not rapidly changing simultaneously. The abundance of a species depends on the trait distribution it possesses, even if that trait distribution is the result of evolution primarily in the very distant past (e.g., see *Enallagma* example above). Likewise, explaining the form and intensity of natural selection at any instant in time must be based on the abundances and traits of interacting species.

When we think of evolution, our minds typically gravitate to the genetics involved, since change in the genetic

composition of a population is the very definition of evolution. However, three of the four primary causes of evolution have fundamental ecological bases. Genetic drift occurs because of the demographics of small populations. Gene flow results from dispersal decisions that individuals make. Most importantly, natural selection is caused by the differential ecological performances of individuals with different phenotypes. The perils of ignoring these ecological mechanisms are most acute for our understanding of natural selection. As I hope this brief inquiry has shown, the dynamics of density and frequency-dependent natural selection are not mystical or unfathomable. Rather, their typical treatments in models focused primarily on genetics are mere caricatures of the rich mechanisms of species interactions that community ecologists have been studying and modeling for almost a century. Moreover, considering only genetic mechanisms as potential causes of evolutionary change prevents us from imagining such possibilities as adaptive peak shifts driven by the dynamics of natural selection or that the differentiation of species would depend on the productivity of the ecosystem. Certainly, the genetic dynamics of evolution can be complicated, but that is no excuse to simplify, neglect, or ignore the ecological processes that drive those genetic dynamics. I look forward to the continuing conceptual unification of ecological and evolutionary dynamics into a robust theory that melds the richness of both genetics and ecology.

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APPENDIX

Sets of Equations Describing the Interaction between Resources and Consumers

In this appendix, I present the sets of models used in simulations to operationalize the interactions between consumers and resources that are explored in the paper. These models describe the abundance and trait dynamics for two resources (indexed $i = 1, 2$) and two consumers (indexed $j = 1, 2$). The abundances of the resources are specified by the general equations set forth in (2), and the trait dynamics are specified by the general equations set forth in (4). In the following, the resource's intrinsic birthrate is a bidirectional independent trait given by (6), and the consumer's intrinsic death rate is a bidirectional independent trait given by (7). In this work, I consider only the situation where the resources have identical parameters and the consumers have identical parameters, and so parameters are not indexed to any particular species. For a more general analysis in which species can differ in parameters, see McPeck (2017). The various models below differ in the types of traits that underlie the attack coefficient.

Attack Coefficient Underlain by Bidirectional Dependent Traits

These abundance and trait dynamic equations are used when the attack coefficient is defined by bidirectional dependent traits specified by equation (8) for a single consumer and a single resource:

$$\begin{aligned}
\frac{dR_i}{dt} &= R_i \left(c_0(1 - \gamma(\bar{z}_{R_i} - \tilde{z}_R^c)^2) - dR - \sum_{j=1}^2 \frac{a_0 e^{-(\bar{\Delta}_j/\beta)^2} N_j}{1 + \sum_{i=1}^2 a_0 e^{-(\bar{\Delta}_j/\beta)^2} hR_i} \right), \\
\frac{dN_j}{dt} &= N_j \left(\sum_{i=1}^2 \frac{ba_0 e^{-(\bar{\Delta}_j/\beta)^2} R_i}{1 + \sum_{i=1}^2 a_0 e^{-(\bar{\Delta}_j/\beta)^2} hR_i} - f_0(1 + \theta(\bar{z}_{N_j} - \tilde{z}_N^f)^2) - gN_j \right), \\
\frac{d\bar{z}_{R_i}}{dt} &= V_{z_{R_i}} \left(-2c_0\gamma(\bar{z}_{R_i} - \tilde{z}_R^c) - \sum_{j=1}^2 \frac{2a_0\bar{\Delta}_j e^{-(\bar{\Delta}_j/\beta)^2} N_j}{\beta^2 (1 + \sum_{i=1}^2 a_0 e^{-(\bar{\Delta}_j/\beta)^2} hR_i)} \right), \\
\frac{d\bar{z}_{N_j}}{dt} &= V_{z_{N_j}} \left(-\sum_{i=1}^2 \frac{2ba_0\bar{\Delta}_j e^{-(\bar{\Delta}_j/\beta)^2} R_i}{\beta^2 (1 + \sum_{i=1}^2 a_0 e^{-(\bar{\Delta}_j/\beta)^2} hR_i)^2} - 2f_0\theta(\bar{z}_{N_j} - \tilde{z}_N^f) \right).
\end{aligned} \tag{A1}$$

In these equations and below, $\Delta_{ji} = z_{N_j} - z_{R_i}$. Other parameters are as defined in the main text.

Attack Coefficient Underlain by Unidirectional Dependent Traits

These abundance and trait dynamic equations are used when the attack coefficient is defined by unidirectional dependent traits specified by equation (9):

$$\begin{aligned}
\frac{dR_i}{dt} &= R_i \left(c_0(1 - \gamma(\bar{z}_{R_i} - \tilde{z}_R^c)^2) - dR - \sum_{j=1}^2 \frac{a_0 N_j / (1 + e^{-\alpha\bar{\Delta}_j})}{1 + \sum_{i=1}^2 (a_0 hR_i / (1 + e^{-\alpha\bar{\Delta}_j}))} \right), \\
\frac{dN_j}{dt} &= N_j \left(\sum_{i=1}^2 \frac{ba_0 R_i / (1 + e^{-\alpha\bar{\Delta}_j})}{1 + \sum_{i=1}^2 (a_0 hR_i / (1 + e^{-\alpha\bar{\Delta}_j}))} - f_0(1 + \theta(\bar{z}_{N_j} - \tilde{z}_N^f)^2) - gN_j \right), \\
\frac{d\bar{z}_{R_i}}{dt} &= V_{z_{R_i}} \left(-2c_0\gamma(\bar{z}_{R_i} - \tilde{z}_R^c) + \sum_{j=1}^2 \frac{2a_0\alpha e^{-\alpha\bar{\Delta}_j} N_j}{(1 + e^{-\alpha\bar{\Delta}_j}) (1 + \sum_{i=1}^2 (a_0 hR_i / (1 + e^{-\alpha\bar{\Delta}_j})))} \right), \\
\frac{d\bar{z}_{N_j}}{dt} &= V_{z_{N_j}} \left(\sum_{i=1}^2 \frac{ba_0\alpha e^{-\alpha\bar{\Delta}_j} R_i}{(1 + e^{-\alpha\bar{\Delta}_j})^2 (1 + \sum_{i=1}^2 (a_0 hR_i / (1 + e^{-\alpha\bar{\Delta}_j})))^2} - 2f_0\theta(\bar{z}_{N_j} - \tilde{z}_N^f) \right).
\end{aligned} \tag{A2}$$

Attack Coefficient Underlain by Unidirectional Independent Traits

These abundance and trait dynamic equations are used when the attack coefficient is defined by unidirectional independent traits specified by equation (10):

$$\begin{aligned}
\frac{dR_i}{dt} &= R_i \left(c_0 (1 - \gamma(\bar{z}_{R_i} - \bar{z}_R^c)^2) - dR_i - \sum_{j=1}^2 \frac{a_0 \bar{z}_R \bar{z}_{N_j} N_j / (\epsilon_R + \bar{z}_{R_i})(\epsilon_N + \bar{z}_{N_j})}{1 + \sum_{i=1}^2 (a_0 \bar{z}_R \bar{z}_{N_j} h R_i) / (\epsilon_R + \bar{z}_{R_i})(\epsilon_N + \bar{z}_{N_j})} \right), \\
\frac{dN_j}{dt} &= N_j \left(\sum_{i=1}^2 \frac{b a_0 \bar{z}_R \bar{z}_{N_j} R_i / (\epsilon_R + \bar{z}_{R_i})(\epsilon_N + \bar{z}_{N_j})}{1 + \sum_{i=1}^2 (a_0 \bar{z}_R \bar{z}_{N_j} h R_i) / (\epsilon_R + \bar{z}_{R_i})(\epsilon_N + \bar{z}_{N_j})} - f_0 (1 + \theta(\bar{z}_{N_j} - \bar{z}_N^f)^2) - g N_j \right), \\
\frac{d\bar{z}_{R_i}}{dt} &= V_{z_{R_i}} \left(-2c_0 \gamma(\bar{z}_{R_i} - \bar{z}_R^c) + \sum_{j=1}^2 \frac{a_0 \epsilon_R \bar{z}_{N_j} N_j / (\epsilon_R + \bar{z}_{R_i})^2 (\epsilon_N + \bar{z}_{N_j})}{1 + \sum_{i=1}^2 (a_0 \bar{z}_R \bar{z}_{N_j} h R_i) / (\epsilon_R + \bar{z}_{R_i})(\epsilon_N + \bar{z}_{N_j})} \right), \\
\frac{d\bar{z}_{N_j}}{dt} &= V_{z_{N_j}} \left(\sum_{i=1}^2 \frac{b a_0 \epsilon_N \bar{z}_{R_i} R_i / (\epsilon_R + \bar{z}_{R_i})(\epsilon_N + \bar{z}_{N_j})^2}{(1 + \sum_{i=1}^2 (a_0 \bar{z}_R \bar{z}_{N_j} h R_i) / (\epsilon_R + \bar{z}_{R_i})(\epsilon_N + \bar{z}_{N_j}))^2} - 2f_0 \theta(\bar{z}_{N_j} - \bar{z}_N^f) \right).
\end{aligned} \tag{A3}$$

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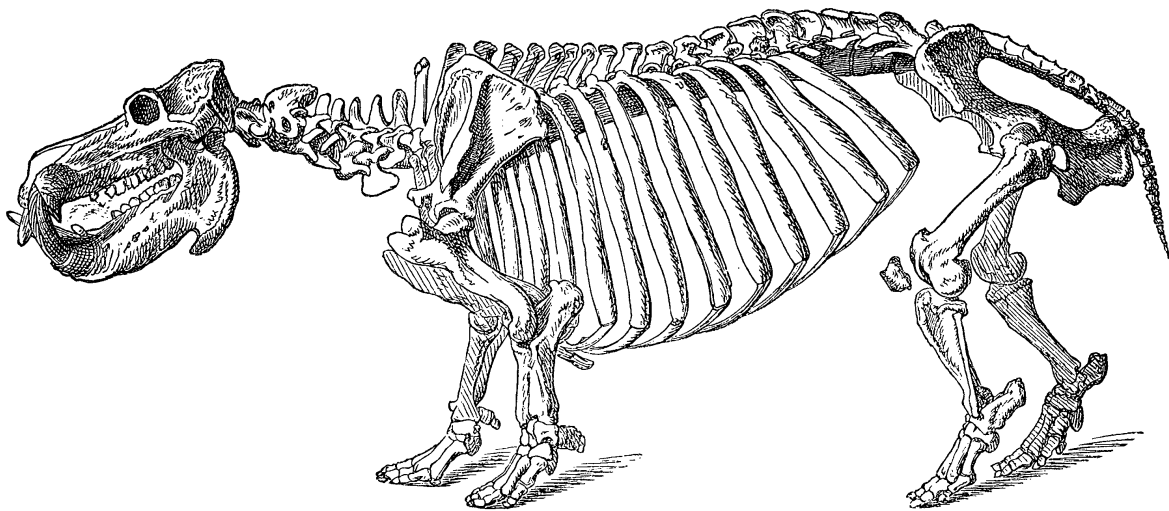
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“The hippopotamus is well drawn, especially its head and face, and its skeleton [figured] is represented, while the account of it by Dr. Brehm is detailed and fresh.” From the review of “Recent Literature: Brehm’s *Animal Life*” (*The American Naturalist*, 1878, 12:682–685).