

Limiting Similarity? The Ecological Dynamics of Natural Selection Among Resources and Consumers Caused By Both Apparent And Resource Competition

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Abstract. Much of ecological theory presumes that natural selection should foster species coexistence by phenotypically differentiating competitors so that the stability of the community is increased, but whether this will actually occur is a question of the ecological dynamics of natural selection. I develop an evolutionary model of consumer-resource interactions based on MacArthur's and Tilman's classic works, including both resource and apparent competition, to explore what fosters or retards the differentiation of resources and their consumers. Analyses of this model predict that consumers will differentiate only on specific ranges of environmental gradients (e.g., greater productivity, weaker stressors, lower structural complexity); and where it occurs, the magnitude of differentiation also depends on gradient position. In contrast to "limiting similarity" expectations, greater intraspecific phenotypic variance results in less differentiation among the consumers because of how phenotypic variation alters the fitness landscapes driving natural selection. In addition, the final structure of the community that results from the coevolution of these interacting species may be highly contingent on the initial properties of the species as the community is being assembled. These results highlight that evolutionary conclusions about community structure cannot be based on ecological arguments of community stability or coexistence, but rather must be explicitly based on the ecological dynamics of natural selection.

Key words: adaptive evolution, apparent competition, character displacement, limiting similarity, resource competition.

Introduction

The idea that species must be different to coexist is embedded in the foundation of community ecology. The clearest initial articulations of this idea were made by Hutchinson in his elaboration of the “Volterra-Gause principle” to express his definition of the niche (Hutchinson 1958) and his hypothesis for why there are so many kinds of animals (Hutchinson 1959). Most explorations of this idea have focused on one particular type of species interaction—competition among consumers for shared resources. Resource competition is an indirect interaction between consumers that is mediated by their effects on and responses to shared resources (Levene 1976; Tilman 1980; 1982; 1987). If multiple resource species are involved, the indirect interaction of apparent competition between resources also occurs and is mediated by their effects on and responses to the consumers (Holt 1977). However, MacArthur’s original exploration of these issues recast all of these indirect interactions into direct interactions between the consumers using the Lotka-Volterra competition framework (MacArthur 1969; 1970; 1972; Schoener 1974; Abrams 1975; Case and Casten 1979; Chesson 1990; Kleinhesselink and Adler 2015; Letten et al. 2017). This recasting remains the pervasive framework for interpreting the community structure of coexisting species (e.g., Chesson 2000; Adler et al. 2007), although many simplifying assumptions must be made (MacArthur 1970; MacArthur 1972; Schoener 1974). However, a number of analyses have shown that these assumptions greatly restrict the range of possible community outcomes that can occur and completely remove the effects of apparent competition, which greatly distorts the effects of one consumer on another (Levene 1976; Chesson 1990; Abrams 1998; Abrams et al. 2008a; Abrams and Rueffler 2009; Kleinhesselink and Adler 2015).

If consumer species that compete for resources must be different to coexist, how different must they be? Hutchinson (1959) originally suggested that a lower limit to species similarity may exist, and MacArthur and Levins (1964; 1967) began the theoretical search in earnest for such a “limiting similarity.” This idea is best encapsulated in May and MacArthur’s (1972) diagram of the degree of niche overlap among a set of consumers feeding on a spectrum of

resources, and how these consumer feeding relationships are recast into Lotka-Volterra competition. They argued that the ratio of the difference between the peaks in the resource utilization curves of adjacent consumers relative to the widths of the utilization curves—their d/w ratio—should have a minimum, limiting value that permits coexistence. The intuitive prediction from this is that if consumer species can utilize a broader spectrum of resources, for example by having broader intraspecific phenotypic distributions, adjacent consumers along the spectrum would have to be more differentiated to permit their coexistence (MacArthur and Levins 1967; May and MacArthur 1972; May 1973; 1974; Roughgarden 1974; Turelli 1978a; b; Abrams et al. 2008a; Abrams et al. 2008b; Abrams and Rueffler 2009; Barabás and D'Andrea 2016) or to decrease the sensitivity of coexistence to perturbations in parameters (Mészéna et al. 2006; Szabó and Mészéna 2006; Szilagyi and Mészéna 2009; Barabás et al. 2012a; Barabás et al. 2012b; Barabás et al. 2014). While no rigid limit of functional overlap between species has been identified (e.g., Abrams 1975; Turelli 1978a; 1981), greater overlap is expected to reduce the likelihood of coexistence (Mészéna et al. 2006). The presumption underlying these ideas is that natural selection should act to promote coexistence by causing species to differentiate in order to reduce competition via reducing niche overlap—character displacement (e.g., Brown and Wilson 1956; Hutchinson 1959; MacArthur and Levins 1967; MacArthur 1970; 1972; Roughgarden 1974; Stuart and Losos 2013).

The other unstated presumption in this line of reasoning is that such differentiation should occur regardless of ecological conditions, because reducing the strength of interspecific resource competition among the consumers is assumed to always be beneficial. However, what will evolve depends on how those ecological conditions shape the selection regime that each species experiences. In an unproductive ecosystem where resources cannot achieve high abundances, the fitness return to a consumer specializing on only one resource species may be less than generalized feeding on multiple resource species, whereas resource specialization may be more profitable in a more productive ecosystem, even with the same array of resource species. Additionally, the apparent competitive indirect effects among resource species will be shaped by

their relative productivities, which may in turn skew how consumers differentiate in response to them (Abrams 1986). Alternatively, other features of the ecosystem in which the species interact may limit consumer abundances (i.e., high intrinsic death rates) or their abilities to exploit the resources (e.g., habitat complexity), which might in turn limit their abilities to depress resource abundances to levels that would favor differentiation to reduce resource competition. These consequences would only be apparent when the ecological context that shapes the strengths of both resource and apparent competition are considered, and the relative strengths of these indirect effects may be as important to determining whether consumer and resource species differentiate as the degree of niche overlap.

A number of studies have addressed these presumptions more directly by building coevolutionary models of competing species to explore whether natural selection causes them to differentiate. Many have utilized modified versions of May and MacArthur's (1972) Lotka-Volterra competition framework in which a continuous spectrum of resources is available that determines the carrying capacities of genotypes or phenotypes based on their utilization functions along that spectrum (Roughgarden 1972; Bulmer 1974; Roughgarden 1976; Slatkin 1980; Matessi and Jayakar 1981; Pacala and Roughgarden 1982; Milligan 1985; Taper and Case 1985; 1992; Doebeli 1996; Ackermann and Doebeli 2004; Scheffer and van Nes 2006; Vasseur et al. 2011; Barabás and D'Andrea 2016). Others have modeled both consumer and resource species explicitly but used fitness set approaches to infer phenotypic differences instead of modeling phenotypes directly (Lawler and Maynard Smith 1976; Lundberg and Stenseth 1985; Abrams 1986; Abrams 1987a; b). Still others have explored how diet composition of the consumers may evolve when feeding on various types of resources (e.g., Abrams 1987b; Vasseur and Fox 2011; Klauschies et al. 2016). Many of these studies find that consumers will differentiate under some circumstances and converge to have the same phenotypic distributions under others. One disconcerting but recurring result is that consumer differentiation occurs when phenotypic variances (measured as the breadths of the utilization functions) are small, but consumers converge when phenotypic variances are large (Bulmer 1974; Roughgarden 1976;

Slatkin 1980; Taper and Case 1985; Ackermann and Doebeli 2004), which would seem to contradict the ecological expectations. However, few of these studies have systematically explored how phenotypic variance affects the likelihood or magnitude of differentiation (but see Taper and Case 1985; Barabás and D'Andrea 2016), or whether various ecological contexts may promote or retard differentiation (for one example, see Abrams 1986).

In this paper, I derive and analyze a model of the abundance and trait dynamics resulting from two consumer species feeding on two resource species (Fig. 1). This is an elaboration of MacArthur's (1969; 1970; 1972) original mechanistic consumer-resource model and of Tilman's (1980; 1982) model of the abundance dynamics of two consumer species feeding on two perfectly substitutable resource species. This is also an extension of the model analyzed by Schreiber et al. (2011) of apparent competition (i.e., one consumer feeding on two resources) in which only the consumer could evolve. In the present model, both consumers and resources evolve in response to one another, and their ecological and evolutionary dynamics are shaped by both the resource competitive indirect effects among the consumers and the apparent competitive indirect effects among the resources (Levene 1976; Leibold 1995; 1998). The community ecologist should see how these indirect effects generate natural selection among a set of interacting consumers and resources, and evolutionary biologists should see that these indirect effects are central to how natural selection is generated among interacting species.

The analyses of the model presented here address three questions. First, what ecological conditions retard or foster the differentiation of resource and consumer species? In particular, I consider whether ecosystem features that shape the productivity of the resources, the mortality of the consumers, or the abilities of consumers to harvest resources will influence the likelihood and magnitude of differentiation. Second, how do levels of phenotypic variance in consumers and resources influence the levels of phenotypic differentiation that occur? Intraspecific phenotypic variation defines variability among conspecific consumers in their abilities to forage on the range of available resources and the degree of resource utilization overlap between the consumer populations. Likewise, phenotypic variation in a resource defines the range of

available resource types to each consumer and so the scope of influence for apparent competition among the resources. Finally, how do trade-offs among traits that influence multiple fitness components shape how consumers and resources will differentiate? A phenotypic trait may experience selection because of its effect on multiple fitness components; how such traits will drive species differentiation depend on the fitness balances within each species that increase their fitness overall and not just in response to selection generated by resource or apparent competition.

Model

Consider the interactions that occur in a community module with two consumer species and two resource species (Fig. 1). Each consumer feeds on both resources, but the consumer species do not interact with one another directly. For example, one can imagine these as two bird species feeding on the seeds of two plant species or two fish species feeding on two zooplankton species. Following MacArthur's (1969; 1970; 1972) and Tilman's (1980; 1982) original approaches to this community module, the two resource species each follow logistic population growth in the absence of any consumers and so do not interact directly with one another, and each consumer has a linear functional response for feeding on each resource. Each consumer also has a density-dependent death rate in the analysis presented here. Each individual of each species has one ecologically important trait that influences both its performance in interactions with individuals of its own species and the other species that determine its overall fitness: traits are identified as z_{R_i} for each resource ($i = 1,2$) and z_{N_j} for each consumer ($j = 1,2$).

From these statements we can derive the equations describing both the abundance and trait dynamics for the four species in this community module. First, assume that the ecologically important trait of each species is normally distributed with a specified mean and variance:

$$p(z_{R_i}) = \frac{e^{-\frac{(z_{R_i} - \bar{z}_{R_i})^2}{2\sigma_{z_{R_i}}^2}}}{\sqrt{2\pi\sigma_{z_{R_i}}^2}} \quad \& \quad p(z_{N_j}) = \frac{e^{-\frac{(z_{N_j} - \bar{z}_{N_j})^2}{2\sigma_{z_{N_j}}^2}}}{\sqrt{2\pi\sigma_{z_{N_j}}^2}}. \quad (1)$$

Furthermore, the phenotypic variance of each species is composed of an additive genetic component ($G_{z_{R_i}}$ and $G_{z_{N_j}}$) which determines the magnitude of evolutionary response to phenotypic selection and an environmental component ($E_{z_{R_i}}$ and $E_{z_{N_j}}$): thus, $\sigma_{z_{R_i}}^2 = G_{z_{R_i}} + E_{z_{R_i}}$ and $\sigma_{z_{N_j}}^2 = G_{z_{N_j}} + E_{z_{N_j}}$ (this assumes no non-additive genetic effects and no genotype by environment interaction effects). Throughout this analysis, I assume that the variance components underlying the phenotypes of each species do not change, and their evolutionary dynamics are adequately described by change in the mean trait value of each species (Lande 1976; 1982; 2007).

The overall fitness of each resource individual is determined by the difference between two underlying fitness components: a density-dependent birth fitness component, and a death fitness component determined solely by the two consumers feeding on it. The density-dependent birth fitness component of each resource is described by a generalized logistic function, $c_i(z_{R_i}) - d_i R_i$. Each resource's intrinsic birth rate, $c_i(z_{R_i})$, is determined by its trait value, and d_i is the rate of decrease in this rate as resource i 's overall abundance increases. The function $c_i(z_{R_i})$ is maximized at $z_{R_i} = \tilde{z}_{R_i}^c$ and decreases as a quadratic function of the distance of the resource's trait value away from this optimum,

$$c_i(z_{R_i}) = c_{0i} \left(1 - \gamma_i (z_{R_i} - \tilde{z}_{R_i}^c)^2 \right), \quad (2)$$

where c_{0i} is the maximum birth rate, and γ_i scales the rate of decrease away from $\tilde{z}_{R_i}^c$. In the absence of consumers, each resource experiences stabilizing selection only on this fitness component that will move the population's trait mean to $\tilde{z}_{R_i}^c$. In the presence of consumers, the selection on this fitness component may create a fitness trade-off with the fitness components affected by consumer feeding if selection on those other fitness components to reduce death rate from consumer feeding favors trait mean movement away from $\tilde{z}_{R_i}^c$. As in purely ecological models of this type, such a logistic growth term for a resource is often interpreted as "birth rate" but this fitness component can also be interpreted as encapsulating all the demographic processes that impinge on the resource besides feeding by the consumers, and not strictly birth rate (e.g., Slobodkin 1961; Rosenzweig and MacArthur 1963; Rosenzweig 1971; Case 2000; Murdoch et

al. 2003). Because I will only consider situations where this function has positive values within the scope of trait distributions, I will continue to refer to it as the “birth fitness” component.

Each resource’s death fitness component is determined by linear functional responses of the consumers feeding on them. The value of the attack coefficient for an individual consumer feeding on an individual resource is assumed to have a Gaussian form determined by the difference between their trait values,

$$a_{ij}(z_{R_i}, z_{N_j}) = a_{0j} e^{-\frac{(z_{N_j} - z_{R_i})^2}{2\beta_j^2}}, \quad (3)$$

where a_{0j} is the maximum value of the attack coefficient for consumer j when $z_{N_j} = z_{R_i}$, and β_j scales the rate at which the attack coefficient decreases away from this maximum for that consumer. Note that this formulation specifies no trait value as best in these interactions: a given change in the trait value of one species may either increase or decrease the attack coefficient depending on the trait value of the other species. Also, the direction of trait change that increases the attack coefficient is different on either side of the trait value of the other species. For example, the ability of a consumer individual to catch and consume a given resource individual may depend on the match between some metric of the trophic structure of the consumer (e.g., bill size of a bird, or gill raker size of a fish) and some measure of size of the resource (e.g., diameter of a plant seed, or body length of a zooplankton species). If the trait values of the two species are identical, when each is measured on an appropriate scale ($z_{N_j} - z_{R_i} = 0$), the attack coefficient is maximized. However, the attack coefficient decreases as the magnitude of the difference in trait values increases: e.g., a bird may have the highest foraging capability on a particular size of seed, but this foraging capability decreases as seed size both decreases and increases away from this optimal size.

From these assumptions, the expected absolute fitness of a resource individual is given by

$$r_{R_i}(z_{R_i}) = c_i(z_{R_i}) - d_i R_i - \sum_{j=1}^2 N_j \int_{-\infty}^{\infty} p(z_{N_j}) a_{ij}(z_{R_i}, z_{N_j}) dz_{N_j}, \quad (4)$$

where the functional response determining the death rate of the resource with this trait value is integrated over each consumer population. Substituting (1)–(3) into (4) and integrating gives the absolute fitness of each resource individual based on its phenotypic trait value

$$r_{R_i}(z_{R_i}) = c_{0i} \left(1 - \gamma_i \left(z_{R_i} - \tilde{z}_{R_i}^c \right)^2 \right) - d_i R_i - \sum_{j=1}^2 \frac{a_{0j} N_j \beta_j}{\sqrt{\sigma_{z_{N_j}}^2 + \beta_j^2}} e^{-\frac{(\bar{z}_{N_j} - z_{R_i})^2}{2(\sigma_{z_{N_j}}^2 + \beta_j^2)}}. \quad (5)$$

The average fitness of each resource population is then found by integrating these individual fitness values over its entire trait distribution.

$$\begin{aligned} r_{R_i} &= \int_{-\infty}^{\infty} p(z_{R_i}) r_{R_i}(z_{R_i}) dz_{R_i} \\ &= c_{0i} \left(1 - \gamma_i \left(\left(\bar{z}_{R_i} - \tilde{z}_{R_i}^c \right)^2 + \sigma_{z_{R_i}}^2 \right) \right) - d_i R_i - \sum_{j=1}^2 \frac{a_{0j} \beta_j N_j}{\sqrt{\sigma_{z_{R_i}}^2 + \sigma_{z_{N_j}}^2 + \beta_j^2}} e^{-\frac{(\bar{z}_{N_j} - \bar{z}_{R_i})^2}{2(\sigma_{z_{R_i}}^2 + 2\sigma_{z_{N_j}}^2 + \beta_j^2)}} \end{aligned} \quad (6)$$

The first two terms in equation (6) comprise the average birth fitness component (i.e., the population's per capita birth rate), and the summation comprises the average death fitness component (i.e., the population's per capita death rate) of the resource population.

Likewise, each consumer individual's fitness is the sum of a birth and a death fitness component. Each consumer's birth fitness component is determined solely by its converting consumed resource individuals into its own offspring: i.e., a linear numerical response for each resource. Each consumer also has a density-dependent death fitness component defined by $f_j(z_{N_j}) + g_j N_j$ (Gilpin 1975; Gatto 1991; Caswell and Neubert 1998; Neubert et al. 2004; Amarasekare 2008; McPeck 2012; 2014). Each consumer's intrinsic death rate, $f_j(z_{N_j})$, is a function of its trait value, and g_j is the rate of increase in its death rate with its overall population size. When $g_j > 0$, the consumer population experiences an additional source of direct density dependence from processes like interference or cannibalism (Polis 1981), physiological stress (Marra et al. 1995; Lochmiller 1996; McPeck 2004) or limitation due to territoriality (Pulliam and Danielson 1991; McPeck et al. 2001) or from other density dependent features not being modeled such as pathogens and diseases (Janzen 1970; Holt and Pickering

1985; Grover 1994; Terborgh 2012) that limits its population in addition to the indirect density dependence that resource limitation imposes.

The function describing $f_j(z_{N_j})$ is minimized at $z_{N_j} = \tilde{z}_{z_{N_j}}^f$ and increases as a quadratic away from this minimum:

$$f_j(z_{N_j}) = f_{0j} \left(1 + \theta_j \left(z_{N_j} - \tilde{z}_{z_{N_j}}^f \right)^2 \right), \quad (7)$$

where f_{0j} is the minimum intrinsic death rate, and θ_j scales the rate of increase in death rate away from the optimum. Consequently, this fitness component always experiences stabilizing selection toward $\tilde{z}_{z_{N_j}}^f$, and so fitness trade-offs may arise if feeding on resources imposes selection on the birth fitness components to move the trait mean away from $\tilde{z}_{z_{N_j}}^f$. As with the resources, the evolutionary outcome of natural selection on the consumer's trait mean will typically result from optimizing selection generated by various selection pressures acting to change the trait in different directions (Arnold and Wade 1984; Travis 1989).

From these assumptions, the fitness of an individual consumer is found by integrating these individual fitness values over the resource trait distributions:

$$r_{N_j}(z_{N_j}) = \sum_{i=1}^2 R_i \int_{-\infty}^{\infty} p(z_{R_i}) b_j a(z_{R_i}, z_{N_j}) dz_{R_i} - f_j(z_{N_j}) - g_j N_j, \quad (8)$$

where b_j is the conversion efficiency that defines the number of consumer offspring produced per resource killed and eaten (each consumer is assumed to have the same conversion efficiency for both resources, but they may differ between consumers). Substituting (1), (3), and (7) into (8) and integrating gives

$$r_{N_j}(z_{N_j}) = \sum_{i=1}^2 \frac{b_j a_{0j} \beta_j R_i}{\sqrt{\sigma_{z_{R_i}}^2 + \beta_j^2}} e^{-\frac{(z_{N_j} - \bar{z}_{R_i})^2}{2(\sigma_{z_{R_i}}^2 + \beta_j^2)}} - f_{0j} \left(1 + \theta_j \left(z_{N_j} - \tilde{z}_{z_{N_j}}^f \right)^2 \right) - g_j N_j. \quad (9)$$

From this, the average fitness of each consumer population is

$$\begin{aligned} r_{N_j} &= \int_{-\infty}^{\infty} p(z_{N_j}) r_{N_j}(z_{N_j}) dz_{N_j} \\ &= \sum_{i=1}^2 \frac{b_j a_{0j} \beta_j R_i}{\sqrt{\sigma_{z_{R_i}}^2 + \sigma_{z_{N_j}}^2 + \beta_j^2}} e^{-\frac{(\bar{z}_{N_j} - \bar{z}_{R_i})^2}{2(\sigma_{z_{R_i}}^2 + \sigma_{z_{N_j}}^2 + \beta_j^2)}} - f_{0j} \left(1 + \theta_j \left((\bar{z}_{N_j} - \tilde{z}_{z_{N_j}}^f)^2 + \sigma_{z_{N_j}}^2 \right) \right) - g_j N_j \end{aligned} \quad (10)$$

The summation in equation (10) comprises the average birth fitness component (i.e., per capita birth rate), and the last two terms comprise the average death fitness component (i.e., per capita death rate) of the consumer population.

The average fitness of each species defines the dynamics of its abundance (Lande 1982; Charlesworth 1994; Lande et al. 2009). From these,

$$\begin{aligned}
\frac{dR_i}{dt} &= R_i r_{R_i} \\
&= R_i \left[c_{0i} \left(1 - \gamma_i \left(\left(\bar{z}_{R_i} - \tilde{z}_{R_i}^c \right)^2 + \sigma_{z_{R_i}}^2 \right) \right) - d_i R_i - \sum_{j=1}^2 \frac{a_{0j} \beta_j N_j}{\sqrt{\sigma_{z_{R_i}}^2 + \sigma_{z_{N_j}}^2 + \beta_j^2}} e^{-\frac{(\bar{z}_{N_j} - \bar{z}_{R_i})^2}{2(\sigma_{z_{R_i}}^2 + 2\sigma_{z_{N_j}}^2 + \beta_j^2)}} \right] \\
\frac{dN_j}{dt} &= N_j r_{N_j} \\
&= N_j \left[\sum_{i=1}^2 \frac{b_j a_{0j} \beta R_i}{\sqrt{\sigma_{z_{R_i}}^2 + \sigma_{z_{N_j}}^2 + \beta_j^2}} e^{-\frac{(\bar{z}_{N_j} - \bar{z}_{R_i})^2}{2(\sigma_{z_{R_i}}^2 + \sigma_{z_{N_j}}^2 + \beta_j^2)}} - f_{0j} \left(1 + \theta_j \left(\left(\bar{z}_{N_j} - \tilde{z}_{N_j}^f \right)^2 + \sigma_{z_{N_j}}^2 \right) \right) - g_j N_j \right]
\end{aligned} \tag{11}$$

This model is equivalent to the basic consumer-resource model assumed by MacArthur (1969; 1970; 1972) before being recast into Lotka-Volterra competition and to the model developed by Tilman (1980; 1982) for perfectly substitutable resources, except that here the parameters of the model are functions of the trait distributions of the interacting species. As in their models, the consumer abundances are limited by the quantities of available resources, and the resource competitive interactions between consumers are indirect effects that are mediated by how each depletes resource abundances. Additionally, consumers may also limit their own abundances directly. Likewise, the apparent competitive interactions between the resources are indirect effects that are mediated by how each inflates consumer abundances.

Because equations (6) and (10) describe the average fitness of each species as a function of its trait distribution, this derivation also provides the machinery to follow the coevolution of these species in response to one another. Following Lande (1976; 1982; 2007), I assume that the evolution of these species can be adequately described by changes in \bar{z}_{R_i} and \bar{z}_{N_j} over time, given the standard quantitative genetic assumptions for the traits (see also Bulmer 1980; Iwasa et

al. 1991; Abrams et al. 1993; Barton et al. 2017). The change in the trait mean over time is then described by the product of the additive genetic variation in the trait and the partial derivative of average fitness with respect to the average trait value:

$$\begin{aligned}
\frac{d\bar{z}_{R_i}}{dt} &= G_{z_{R_i}} \frac{\partial r_{R_i}}{\partial \bar{z}_{R_i}} \\
&= G_{z_{R_i}} \left[-2c_{0i}\gamma_i (\bar{z}_{R_i} - \bar{z}_{R_i}^c) - \sum_{j=1}^2 \frac{a_{0j}\beta_j N_j (\bar{z}_{N_j} - \bar{z}_{R_i})}{(\sigma_{z_{R_i}}^2 + \sigma_{z_{N_j}}^2 + \beta_j^2)^{3/2}} e^{-\frac{(\bar{z}_{N_j} - \bar{z}_{R_i})^2}{2(\sigma_{z_{R_i}}^2 + \sigma_{z_{N_j}}^2 + \beta_j^2)}} \right] \\
\frac{d\bar{z}_{N_j}}{dt} &= G_{z_{N_j}} \frac{\partial r_{N_j}}{\partial \bar{z}_{N_j}} \\
&= G_{z_{N_j}} \left[\sum_{i=1}^2 -\frac{ba_{0j}\beta_j R_i (\bar{z}_{N_j} - \bar{z}_{R_i})}{(\sigma_{z_{R_i}}^2 + \sigma_{z_{N_j}}^2 + \beta_j^2)^{3/2}} e^{-\frac{(\bar{z}_{N_j} - \bar{z}_{R_i})^2}{2(\sigma_{z_{R_i}}^2 + \sigma_{z_{N_j}}^2 + \beta_j^2)}} - 2f_{0j}\theta_j (\bar{z}_{N_j} - \bar{z}_{N_j}^f) \right]
\end{aligned} \tag{12}$$

Together, equations (11) and (12) describe an evolutionary elaboration of MacArthur's (1969; 1970; 1972) and Tilman's (1980; 1982) mechanistic models of two consumer species feeding on two resource species. Obviously, this system of eight differential equations describing their joint abundance and mean trait dynamics is analytically intractable, and an exhaustive analysis is beyond the scope of a single paper. Therefore, I will analyze the resulting dynamics numerically, and present results from interesting areas of parameter space to address the three questions expounded at the end of the Introduction. (The code for this numerical exploration was written in Matlab and is available in the electronic appendix.)

Results

As in simpler models of consumer-resource coevolution, differences in most parameters among species on a specific trophic level will foster differentiation (McPeck 2017b). Therefore, I restrict the analyses presented here to situations where the consumer species have identical underlying parameter values (i.e., $c_{01} = c_{02}$, $a_{01} = a_{02}$, $\theta_1 = \theta_2$, $\sigma_{z_{N_1}}^2 = \sigma_{z_{N_2}}^2$, etc.), except to address issues about differences in specific parameters. Also, alternative stable equilibria are

apparent in some areas of parameter space: i.e., alternative stable outcomes result from different initial mean trait values. In general, I began the numerical simulations presented here with the consumers near their intrinsic death optima (i.e., $\bar{z}_{N_j} \approx \tilde{z}_{z_{N_j}}^f$) and at very low abundances, and with the resources very near their intrinsic birth optima (i.e., $\bar{z}_{R_i} \approx \tilde{z}_{z_{R_i}}^c$) and at their equilibrium abundances for the absence of the consumers: this simulates invasion by the two consumers of a community consisting of the two resources. However, I did explore the effects of other sets of initial conditions, and I will note whether different initial mean trait values resulted in the community approaching different locally stable equilibria.

To build intuition into the dynamics of differentiation, first consider the abundance and trait dynamics of a parameter combination that results in the differentiation of identically parameterized resources with a single consumer (see also Schreiber et al. 2011). In this example, the phenotypic optima of the resources' intrinsic birth rates and the consumer's intrinsic death rate are identical (i.e., $\tilde{z}_{R_1}^c = \tilde{z}_{R_2}^c = \tilde{z}_{N_1}^f$). For the resources to differentiate, their initial trait means must straddle those of the consumer. The consumer imposes disruptive selection on the death fitness component of both resources, with the nadir at the mean trait value of the consumer. Thus, because the consumer's trait mean is between those of the resources, the resources evolve to differentiate. Otherwise, if the trait means of the resources are both on the same side of the consumer's trait mean, both resources evolve away from the consumer in the same direction, resulting in the resources not differentiating. If the resources differentiate from one another, the consumer evolves to be a generalist with a trait mean that is intermediate between the two resources and so feeds equally on both (Fig. 2). In this case, the consumer occupies a stable fitness minimum (Abrams et al. 1993) at the nadir between the two fitness peaks on its fitness topography, which are each near the phenotypic means of the two resources (Fig. 2). This fitness minimum is a stable equilibrium, because perturbations of the consumer's trait distribution in either direction will cause changes in resource abundances that will alter the selection gradients on the consumer's two birth fitness components to return it to this equilibrium. Specifically, if the consumer is perturbed towards one of the resources, it depresses the abundance of that

resource, and the abundance of the other resource increases because of the reduced feeding pressure. Selection then favors the consumer to evolve towards the resource whose abundance increased and so back to the stable fitness minimum.

Now consider the same situation, but with an additional identically parameterized consumer (i.e., two consumers and two resources). Again, the resources will only differentiate if their initial trait means straddle those of the two consumers. Once the resources differentiate, the fitness surfaces of both consumers have two fitness peaks, because their birth fitness components experience disruptive selection; and if their trait means are not identical, the fitness nadir is positioned between them because of the same density-dependent and frequency-dependent selective forces due to resource depletion by the two consumers that caused the stable fitness minimum for only one consumer. However, with two consumers present, selection then pushes the two consumers apart because each can increase its overall fitness by evolving towards the resource whose abundance is not being depressed by the other consumer. As a result, the two consumers will differentiate so that each has a much higher realized attack coefficient on one resource and so feeds primarily on that resource (Fig. 3). At the joint ecological and evolutionary equilibrium in this case, the resources and the consumers all occupy fitness peaks (Fig. 3A-D). (The changes in the trait means and abundances of the species cause the shapes of the fitness surfaces experienced by each species to change over the course of the simulation. An animation of Figure 3 showing these dynamics is available in the Electronic Appendix.)

The phenotypic distributions of the four species at equilibrium are substantially differentiated from one another (Fig. 3E), but simply comparing the phenotypic distributions is deceptive. The appropriate comparison is the functional phenotypic distributions that define their interactions with the other species (Taper and Case 1985): in this case, the distributions with variance parameters $\sigma_{z_x}^2 + \beta_j^2$, where x identifies the species. The overlap of the consumers' functional phenotypic distributions is much greater and more fairly represented by what is being compared in ideas of "limiting similarity."

What ecological conditions retard or foster the differentiation of resource and consumer species? — The ecological context in which these species interactions occur influences whether the resources and consumers will differentiate from one another to reduce apparent and resource competition. Specifically, the effects of various abiotic conditions are encapsulated in the parameters of this model. For example, in the absence of the consumers, the resource species equilibrate at abundances of $R_i^* = c_{0i}/d_i$. If the productivity of the ecosystem in which this community is embedded influences the maximum intrinsic birth rates of the resources (i.e., c_{0i}), more resources will be available to consumers in more productive ecosystems that cause larger values of c_{0i} . Likewise, other types of environmental features, such as water turbidity in aquatic systems or habitat structural complexity in most systems, will cause different values of the maximum attack coefficient (i.e., a_{0j}) to differ among communities found in different locations. Still other environmental features (e.g., stressors, pathogens) may cause differences in the consumers' minimum intrinsic death rates (i.e., f_{0j}) across communities that develop in different locations. Thus, differentiation of identically parameterized species at each trophic level across ranges of these parameters identifies ranges of environmental conditions that promote or retard species differentiation.

Figure 4 shows the equilibrium trait means and population sizes for the four species over ranges of these three different parameters that correspond to important environmental gradients. First, consider the coevolutionary outcomes in ecosystems that differ in productivity (i.e., communities that develop at different points along a gradient of c_{0i}). In communities with lower values of c_{0i} (e.g., $c_{0i} < 0.75$ in Figs. 4A-B), the resources differentiated because of the feeding pressures of the consumers. However, the consumers did not differentiate, because the resources were not abundant enough to provide sufficient fitness returns from feeding primarily on one: the overall fitness surfaces for both consumers had only one fitness peak (e.g., Fig. 4G). Thus, in communities with productivities in this range, the consumers would be ecologically equivalent “neutral” generalists with identical phenotypic distributions that occupy the same functional position in the community and thus have identical effects on the other species in the community

(Leibold and McPeck 2006; McPeck 2017b) (Figs. 4A-B). If the resources' maximum intrinsic birth rates were above this range, the resources were abundant enough at equilibrium to generate two fitness peaks in the consumers' overall fitness surfaces, and so the consumers differentiated from one another (e.g., Fig. 4H). Moreover, the consumers differentiated to a greater extent at higher productivity levels (i.e., higher values of c_{0i}) (Fig. 4A).

A similar pattern of differentiation also emerged along gradients of the maximum attack coefficient. The maximum attack coefficient (a_{0j}) for consumers may depend on structural features of the environment in which these interactions take place. For example, fish feeding on their prey in lakes with turbid water may have lower maximum attack coefficients than the same fish feeding on the same prey species in other lakes with clear water. Ecosystems with greater degrees of structural complexity will also reduce the maximum attack coefficients of consumers foraging for resource species. When the maximum attack coefficients were lower, the consumers did not differentiate (e.g., $a_{0j} < 0.125$ in Figs. 4C-D), but both resources and consumers did differentiate when the maximum attack coefficients were higher (e.g., $a_{0j} > 0.125$ in Fig. 4C-D). Again, the difference between these two regions of parameter space is whether the consumers' overall fitness surfaces have one peak or two, and higher values of the attack coefficients in the two-peak area cause the fitness peaks to be farther apart at equilibrium.

Finally, ecosystems may differ in the minimum intrinsic death rates of the consumers (f_{0j}) because of varying levels of abiotic stressors or different types or abundances of their own enemies (e.g., pathogens, predators). Consumers differentiated along the lower stress range of the gradient (e.g., $f_{0j} < 0.6$ in Fig. 4E-F), but did not differentiate if the f_{0j} 's were higher (e.g., $f_{0j} > 0.6$ in Fig. 4E-F). With higher minimum intrinsic death rates, the shape of the death fitness component dominates the shape of the overall fitness topography, which forces a single adaptive peak for consumers.

In all the communities illustrated in Figure 4, the resources and consumers only differentiated at each trophic level if the initial resource trait means began straddling the trait means of the consumers. Alternatively, if the resources both began on the same side of the consumers'

phenotypes, the resources did not differentiate, but rather evolved away from the consumers in the same direction. In these latter cases, the endpoint was two resources with identical trait means and two consumers with identical trait means that were slightly offset from the resources in the direction of $\tilde{z}_{N_j}^f$. Also, if only one consumer species was present (as in Fig. 2), the single consumer occupied a peak in the overall fitness landscape in the gradient ranges where the two consumers would not differentiate and occupied a stable fitness minimum in the gradient ranges where the two consumers would differentiate.

Differences in specific parameters between either the resources or consumers, which reflect differences in their ecological performances or differences in other features of their biology, also shape how consumers evolve in response to phenotypically differentiated resources. From a community ecology perspective, these differences cause differences in the strengths of the indirect interactions propagated from each species in the community: e.g., when the consumers have fundamental differences in their resource competitive abilities or when the resources have fundamental differences in their apparent competitive abilities. These examples thus illustrate how species will respond to asymmetries in the indirect effects from different species. To better illustrate the main results here, I will consider the situation where the intrinsic birth optima of the resources straddle the intrinsic death optima of the consumers, but the consumers' intrinsic death optima are the same (i.e., $\tilde{z}_{R_1}^c < \tilde{z}_{N_1}^f = \tilde{z}_{N_2}^f < \tilde{z}_{R_2}^c$). This relationship causes the resources to always differentiate from one another regardless of initial trait means. In what follows in this section, I explore how a difference in one other parameter influences how the consumers evolve.

In this model, the potential apparent competitive ability of a resource mediated through a specific consumer is defined by the ratio of its intrinsic birth rate to the attack coefficient from that consumer (i.e., $c_i(z_{R_i})/a_j(z_{R_i}, z_{N_j})$): the resource with the higher ratio is the better apparent competitor mediated through that consumer, because it can maintain a population at a higher consumer abundance (Holt 1977). If the two resource species differ in c_{0i} but all other parameters (except their intrinsic birth optima) are the same, the resource with the larger c_{0i} is then the better potential apparent competitor mediated through both consumers. Differences in

c_{0i} between the two resources would exist if they differ in their abilities to garner their own resources or if the resources that limit their abundances differ in availability. When this difference was extremely large (e.g., $c_{01} < 0.06$ while $c_{02} = 3.0$ in Fig. 5A), the poorer apparent competitor—resource 1 in this case—was driven extinct because the better apparent competitor inflated the consumers’ abundances above levels at which the poorer apparent competitor could maintain a population. If the initial consumer trait means both began between the resource trait means, the two consumers adapted to be specialists feeding primarily on the superior apparent competitive resource. If the consumer trait means began outside the range of the resource trait means, the consumer that was initially closer to the better apparent competitive resource adapted faster and in so doing typically drove the other consumer extinct, and this surviving consumer evolved to the same trait mean feeding primarily on the better apparent competitive resource. At intermediate levels of this difference (e.g., $0.06 < c_{01} < 0.55$ in Fig. 5A), the inferior apparent competitive resource could invade and coexist, but one or both consumers (depending on their initial trait means) adapted to feed primarily on the superior apparent competitive resource. The consumers differentiated to feed primarily on only one resource when the asymmetry in apparent competitive ability between the resources was not substantial (e.g., $c_{01} > 0.55$ in Fig. 5A).

The resource competitive ability of a consumer for a specific resource is defined by the ratio $f_j(z_{N_j}) / (a_j(z_{R_i}, z_{N_j})b_j)$: the consumer that has the lower value of this ratio is the better competitor for that resource (i.e., the R^* rule) (Tilman 1980; 1982). Thus, if the two consumers differ in their f_{0j} but have all other parameters identical, the consumer with the lower f_{0j} is the better resource competitor for both resources. Differences in f_{0j} may exist because of intrinsic physiological differences between the consumer, or because they have different levels of enemies (e.g., specialized predators or pathogens) that cause their intrinsic death rates to differ. If the difference in f_{0j} was large (e.g., $f_{01} < 0.069$ or $f_{01} > 0.306$ in Fig. 5B), the superior resource competitive consumer would drive the other consumer extinct and adapt as a generalist feeding on both resources at a stable fitness minimum. The poorer resource competitor, even though it adapted as best it could, was driven extinct because the superior

resource competitor depressed the abundances of the resources below levels at which the poorer resource competitor could maintain a population. Only when the difference in resource competitive ability was not large (e.g., $0.069 < f_{01} < 0.306$ in Fig. 5B) would both coexist as differentiated consumers.

A difference in the attack coefficients affects both the resources' apparent competitive abilities and the consumers' resource competitive abilities. Increasing the attack coefficient of a consumer on one resource increases the resource competitive ability of that consumer, but decreases the apparent competitive ability of that resource (see above). The maximum attack coefficients of the two consumers may differ (i.e., $a_{01} \neq a_{02}$) because of other traits that affect prey capture that are not being modeled. Because of the opposing effects on resource and apparent competitive abilities of the interacting species, a difference in the maximum attack coefficient between consumers had relatively little effect on the qualitative outcome of consumer evolution because of these opposite effect on the resource competitive and apparent competitive abilities (Fig. 5C). Only when the maximum attack coefficient of one consumer was very near zero would the consumers not differentiate to focus on different resources (e.g., $a_{01} < 0.05$ in Fig. 5C). When the consumers differentiated, the main difference in the resulting community was in species abundances. The consumer having the lower maximum attack coefficient had a higher abundance because the resource on which it specialized equilibrated at a higher abundance.

One prominent conclusion from analyses of models of Lotka-Volterra competition is the importance of the strengths of intraspecific density dependence for the consumers relative to interspecific effects (e.g., MacArthur 1972; Chesson 2000; Adler et al. 2007). This general statement can be made about this formulation of resource competition as well, but direct consumer intraspecific density dependence (i.e., $g_j > 0$) has very different effects in this model as compared to Lotka-Volterra competition formulations. When both consumers had identical strengths of direct density dependence for their death rates, they adapted symmetrically to focus on the different resources (e.g., $g_1 = g_2 = 0$ in Fig. 5D, but any low level of intraspecific density

dependence where they were equal gave comparable results). As the strength of density dependence was increased in only one consumer (consumer 1 in Fig. 5D) but held constant in the other, the consumer with the stronger intraspecific density dependence had a much lower abundance (e.g., McPeck 2012) and adapted as a specialist on one resource, while the other consumer had a much higher abundance and adapted as a generalist feeding roughly equally on both resources again at a stable fitness minimum (Fig. 5D). Only at extremely large differences would the consumer with stronger direct intraspecific density dependence be driven extinct.

How do levels of phenotypic variance in consumers and resources influence the levels of differentiation that occur? — The theory of limiting similarity predicts that consumers should be differentiated from one another to reduce competition for shared resources (MacArthur and Levins 1967; MacArthur 1969; 1970; May and MacArthur 1972; Abrams 1983; Meszena et al. 2006; Abrams and Rueffler 2009; Szilagyi and Meszena 2009). Because the degree of functional overlap between the consumers is the issue, consumers with larger functional phenotypic variances are expected to have their mean trait values displaced farther apart to maintain the same level of overlap (May and MacArthur 1972).

Increasing the consumers’ phenotypic variances in this model does not produce this result; it produced just the opposite. First, consider how the equilibrium mean trait values of the four species change with different levels of environmental variance ($E_{z_{N_j}}$) for the two consumers (Fig. 6). For the parameters considered in Figure 3, higher values of $E_{z_{N_j}}$ caused the consumers to differentiate less from one another (Fig. 6A). Moreover, above a specific value of $E_{z_{N_j}}$ (i.e., $E_{z_{N_j}} > 1.8$ in Fig. 6A), the consumers did not differentiate at all: the consumers co-occurred as ecologically identical “neutral” species in an apparent competition community module.

This was also true when the resources’ intrinsic birth optima straddled the consumers’ intrinsic death optima (Fig. 6B): in this case the resources differentiated from one another to a much greater degree, but higher values of $E_{z_{N_j}}$ still caused the consumers to differentiate less from one another. The equilibrium phenotypic distributions for three levels of $E_{z_{N_j}}$ from Fig. 6B

that result in consumer differentiation are shown for comparison in Figs. 6C-E. The same was also true if the consumers' $E_{z_{N_j}}$ were held constant and the resources' $E_{z_{R_i}}$ were varied (results not shown). I could find no area of parameter space where consumers differentiated more from one another as $E_{z_{R_i}}$ or $E_{z_{N_j}}$ were increased, and the convergence of their phenotypes always occurred smoothly with increasing $E_{z_{R_i}}$ or $E_{z_{N_j}}$.

In the examples shown in Figure 6, the species at each trophic level had identical phenotypic variances. The results were qualitatively identical when the species at each trophic level had very different levels of phenotypic variation. For example, when all other parameters are as in Fig. 6B and the environmental phenotypic variation for N_1 is held constant at $E_{z_{N_1}} = 4.0$, the two consumers differentiated to specialize on the different resources over the range of $E_{z_{N_2}} = 0.0 - 62.1$ (cf. Barabás and D'Andrea 2016).

The consumers differentiated from one another because of how all the direct and indirect interactions that propagate through this community module determine the fitness topography that shapes the evolution of each species (Fig. 6F-H). With little environmental variation in their phenotypes, the consumers' fitness surfaces had two well defined peaks resulting from the clear fitness advantages for specializing on one resource that were apparent in their birth fitness component surfaces (Fig. 6F). With increasing $E_{z_{N_j}}$, the increasing breadth of the functional phenotypic distribution caused the fitness gradients all along the consumers' birth fitness surfaces to become shallower (note the change in the consumers' birth fitness component surfaces in Fig. 6F-H). The result was that trait values where the selection gradients on birth and death fitness components balance (i.e., the overall fitness peaks) moved closer together and the fitness valley between them became shallower. This occurred until a level of $E_{z_{N_j}}$ was reached where the two peaks in overall fitness collapsed into one, and selection moved the two consumers to this common fitness peak (Fig. 6A-B).

How do intraspecific trade-offs among fitness components influence how consumers and resources will differentiate? — The overall form that natural selection takes is defined by the

balance that is struck among the selection gradients of different underlying fitness components (Arnold and Wade 1984; Travis 1989; McPeck 1996). In the present context, this means that how consumers and resources may adapt to one another will be influenced by the forms of selection gradients acting on the fitness components not directly involved in predator evasion or prey capture, i.e., the resources' birth fitness components and the consumers' death fitness components, respectively. To this point, I have considered situations where either the components of selection acting on these fitness components in the resources and consumers all favor the same trait values (i.e., $\tilde{z}_{R_1}^c = \tilde{z}_{R_2}^c = \tilde{z}_{N_1}^f = \tilde{z}_{N_2}^f$) or the traits favored by selection on the resources' birth fitness components straddle the traits favored by selection on the consumers' death fitness components (i.e., $\tilde{z}_{R_1}^c < \tilde{z}_{N_1}^f = \tilde{z}_{N_2}^f < \tilde{z}_{R_2}^c$). All else being equal, these relationships favor the consumers differentiating symmetrically onto the different resources (e.g., Figs. 3, 4 and 6). However, consumers do not differentiate symmetrically if the resources' intrinsic birth optima lie far enough away from the consumers' intrinsic death optima (i.e.,

$$\tilde{z}_{R_1}^c \ \& \ \tilde{z}_{R_2}^c \ll \tilde{z}_{N_1}^f \ \& \ \tilde{z}_{N_2}^f \ \text{or} \ \tilde{z}_{R_1}^c \ \& \ \tilde{z}_{R_2}^c \gg \tilde{z}_{N_1}^f \ \& \ \tilde{z}_{N_2}^f).$$

Figure 7 presents instructive examples of this situation. In all the simulation results presented in Figure 7, the initial trait means of the four species were $\bar{z}_{R_1} = 21.0$, $\bar{z}_{R_2} = 21.2$, $\bar{z}_{N_1} = 17.0$, and $\bar{z}_{N_2} = 17.1$. At low levels of $V_{z_{N_j}}^e$ (e.g., $V_{z_{N_j}}^e < 1.5$ in Fig. 7A), one consumer evolved to be a specialist feeding almost exclusively on one resource, and the other consumer evolved to be a generalist feeding on both resources approximately equally (Fig. 7B). Each consumer occupied a different fitness peak in this range (Fig. 7E). However, note that when two peaks existed in the consumers' overall fitness surfaces, the underlying birth fitness components were not two-peaked for a generalist and a specialist (Fig. 7E). Even though both their birth and death fitness components experienced directional selection across their entire phenotypic range, the subtle curvature in both resulted in a two-peaked overall fitness landscape that caused them to differentiate. Also, in this case, initial trait means had no effect on the outcome of selection. Because of the balances struck between their two underlying fitness components, the resources evolved to match and then cross the phenotypic distributions of the consumers if need be to reach

the single stable equilibrium configuration for a given parameter combination. At intermediate $V_{z_{N_j}}^e$ levels (e.g., $1.5 < V_{z_{N_j}}^e < 3.8$ in Fig. 7A), the consumers did not differentiate, but rather converged to an intermediate generalist phenotype (Fig. 7C). Interestingly, the consumers evolved to and occupied the stable fitness minimum that ranged from 21.80-21.82 depending on the exact level of phenotypic variance (Fig. 7F). At high $V_{z_{N_j}}^e$ levels (e.g., $V_{z_{N_j}}^e > 4.0$ in Fig. 7A), neither the consumers nor the resources differentiated (Fig. 7D). In this parameter range, the consumers' overall fitness peaks finally had a single peak. However, the resources evolved to and occupied a stable fitness saddle point, again resulting from the frequency- and density-dependent feedbacks among the species abundances and mean trait values (Fig. 7G).

However, the outcomes for the various parameter combinations considered in Figure 7 were very different if the resources began as differentiated species with trait means that were far from their intrinsic birth optima. If the resources' trait means were initially far apart and straddled the consumers' trait means, the consumers differentiated as a generalist and specialist for all the phenotypic variance values depicted in Figure 7A. However, if the consumers' initial trait means began outside of the range of the resources' trait means, the outcomes were again as depicted in Figure 7A. Here again, the initial trait distributions of the community members as the community is assembled can strongly influence the community structure that evolves.

Discussion

The analysis of this model clearly demonstrates that purely ecological or purely evolutionary perspectives cannot explain the rich set of possible coevolutionary outcomes for the community structure of two consumers feeding on two resources. Their abundance and trait dynamics cannot be decomposed to be studied separately, and one does not have primacy over the other in effect. Ecologists have realized that the coevolution of interacting species can have profound ramifications on the same magnitudes and on the same time scales as abundance responses (e.g., Yoshida et al. 2003; Fussmann et al. 2007; Kokko and López-Sepulcre 2007; Harmon et al. 2009; Schoener 2011; Bassar et al. 2012; Urban et al. 2012; Travis et al. 2014; Urban and

Richardson 2015). However, the converse is also true that the coevolutionary dynamics of species depend critically on how ecological context shapes the abundances of those interacting species (Hutchinson 1965; Drossel et al. 2001; McPeck 2017b).

One area where the importance of ecological context is clearest is consumer differentiation along parameter gradients that can be interpreted as environmental gradients (Fig. 4). Previous studies generally all noted that consumer differentiation was not inevitable, but few identified any ecological context to when differentiation may or may not be favored (e.g., Lawler and Maynard Smith 1976; Roughgarden 1976; Slatkin 1980; Pacala and Roughgarden 1982; Taper and Case 1985; Abrams 1986). Along a productivity gradient (i.e., c_{0i}), consumer differentiation only occurred when the resource species were at high enough abundances to provide a sufficient overall fitness advantage for feeding primarily on one over generalized feeding on both (Figs. 4A-B). Abrams (1986) found a similar relationship using a fitness set approach. Along a stressor gradient of consumer minimum death rate (i.e., f_{0j}) (e.g., abiotic stressors or the abundances or types of various enemies like herbivores, predators, or diseases that are subsumed into the consumer's death rate in this model), consumers also showed a consistent pattern of differentiation or lack thereof (e.g., Figs. 4E-F). When a consumer's death rate is high, the shape of its death fitness component surface dominates the shape of the overall fitness surface and so overrides any fitness advantages from feeding specialization (McPeck 1996). Consumer differentiation is also predicted to differ among communities that develop in areas that differ in habitat structural complexity (e.g., a_{0j}) that would affect the abilities of consumers to kill and consume the resources (e.g., Figs. 4C-D). Thus, while phenotypically differentiated resource species are necessary for consumer differentiation, consumers are predicted to differentiate to feed primarily on one resource only in more productive and more benign ecosystems and in ecosystems where the resources are easier to harvest, even if differentiated resources are available all along these gradients.

The results of these analyses also strongly argue that a purely ecological analysis of consumer differentiation is also insufficient. Schreiber et al. (2011) analyzed a comparable

model with one consumer and two resources, and they illustrated a rich set of consequences for both resources and the consumer in the final community, including apparent competition, apparent facilitation and “apparent competitive” exclusion, depending on the level of consumer’s phenotypic variance and initial trait distributions. The original motivation for this work was to extend their model to test whether the predictions of the theory of limiting similarity are supported when consumers and resources can all evolve in response to one another. Ecological derivations of the idea of a limiting similarity among resource competitors predict that coexistence is less likely with greater overlap of their phenotypic distributions (MacArthur and Levins 1967; MacArthur 1970; MacArthur 1972; May and MacArthur 1972; May 1974; Roughgarden 1974; Abrams 1975; Turelli 1978a; Abrams 1983; Meszena et al. 2006; Abrams and Rueffler 2009). As a result, evolution is expected to push consumers apart to reduce interspecific competition—character displacement—and thus promote their coexistence (Brown and Wilson 1956; Hutchinson 1959; MacArthur and Levins 1967; MacArthur 1970; 1972; Roughgarden 1974; Stuart and Losos 2013).

In contrast to this expectation based purely on ecological considerations, increasing the phenotypic variances in this model decreased the degree to which consumers differentiated, and above some level the two consumers converged to identical generalist trait distributions (Fig. 6). Moreover, a stable community resulted no matter the level of phenotypic variability in the species and no matter the degree of differentiation. Previous studies based on Lotka-Volterra competition dynamics also found that consumer differentiation only occurred at lower levels of phenotypic variance and character convergence happened at high levels (Bulmer 1974; Roughgarden 1976; Slatkin 1980; Taper and Case 1985; Ackermann and Doebeli 2004). For example, in the most detailed model constructed by Taper and Case (1985; i.e., their “Free WPNW Model”), they created a spectrum of non-evolving resources that could be depleted in abundance, but the consumers had within-individual and between-individual variances in resource exploitation abilities that could evolve, and the mean position of the entire consumers’ distributions could evolve. The genetic components of phenotypic variance eventually evolved

to zero, leaving only environmental components of phenotypic variation in the consumers. Consumers differentiated less when the environmental components of their phenotypic variances were greater, and consumers converged to the same mean phenotype at high levels of environmental phenotypic variances (see Fig. 8 in Taper and Case 1985), as was found for the present model. I also explored whether temporal variation in the parameters (e.g., at each time step of a simulation drawing c_{0i} randomly from a normal distribution with a specified mean and variance) affected the degree of differentiation (May and MacArthur 1972; May 1974; Turelli 1978a; b; 1981), and found that such temporal environmental variation had no effect on how species evolved (results not shown).

If two consumers are present and they differentiate, the critical issue determining how much they will differentiate from one another is how far the two fitness peaks are from one another (Fig. 6F-H). Increasing the phenotypic variance of a consumer decreases the strength of the selection gradients on its birth fitness component (i.e., the feeding-related fitness component) across the range of its phenotype in two ways. First, a higher frequency of individuals with lower fitnesses are included, which lowers average fitness particularly near optimal trait values (e.g., note the decrease in the height of the average death fitness surface with increasing levels of $V_{z_{N_j}}^e$ in Figs. 6F-H). Second, a broader phenotypic distribution will decrease the depth of the fitness valley between the two peaks because a greater fraction of phenotypes that receive higher returns for foraging on both resources will exist in the population (e.g., compare the consumers' birth and overall fitness surfaces in Figs. 6F-H); as a result, the selection gradients all along the birth fitness component surface are shallower. Because the peaks in the overall fitness landscape occur where the selection gradients on the various fitness components balance (i.e., \bar{z}_x values where $\partial r_x / \partial \bar{z}_x = 0$ in equations (12)), the overall fitness peaks are also closer together with higher phenotypic variance.

The dynamics of consumer differentiation is driven by ecological dynamics analogous to what causes a single consumer to occupy a stable fitness minimum in Figure 2 (Abrams et al. 1993). If the trait mean of the single consumer is perturbed away from this equilibrium towards

one resource, the consumer depresses the abundance of that resource, and the abundance of the other resource increases because of the reduced feeding pressure on it. As a result, selection now favors the consumer evolving towards the resource with higher abundance, and so back to towards the equilibrium. These resource abundance responses to the change in the consumer's mean trait value are what make this equilibrium stable (Fig. 2). With two consumers are present (e.g., the scenario illustrated in Fig. 3), selection favors each consumer evolving away from the other consumer that is depleting resources and so toward the resource with trait mean away from that of the other consumer that the competitor is not depleting. When the differentiation process begins, each consumer is depressing the abundances of the resources with trait values near its trait mean most, and so each consumer's birth fitness component has a fitness nadir between it and the other consumer. Consequently, each consumer's overall fitness increases in the direction that is away from the other consumer because of higher resource abundances in that direction. Consumer differentiation proceeds until the selection gradients on their respective birth and death fitness components balance (i.e., the various terms in the square brackets in each equation of (12) sum to zero such that $\partial r_x / \partial \bar{z}_x = 0$) (Lande 1976; Felsenstein 1979; Lande 1982; Iwasa et al. 1991; Abrams et al. 1993; McPeck 1996; 2017b; a). Interestingly, the same overall dynamics driving differentiation to different fitness peaks can occur when both consumers experience overall directional selection on their birth fitness components, if the curvatures of the underlying birth and death fitness components will produce multiple peaks in the overall fitness topography (e.g., Fig. 7E). Thus, consumer differentiation is driven by the selection pressures that are generated by the indirect effects caused by both resource and apparent competition that propagate through this community module to shape the dynamics of the species' overall fitness topographies (Abrams et al. 1993; McPeck 2017b; a).

The range of selection dynamics producing convergence of consumers to the same generalist phenotype can be just as diverse. In many cases, convergence results when the disruptive selection on each consumer's birth fitness component is weaker than the stabilizing selection acting on their death fitness component, resulting in a single fitness peak for each at the same

trait mean (e.g., Fig. 4G). In other cases, the consumers converge to the same fitness maximum that results from optimizing selection caused by directional selection pressures pushing different fitness components in opposing directions (e.g., Fig. 7G) (Travis 1989). In still other cases, two consumers may evolve to and occupy the same stable fitness minimum (e.g., Fig. 7F). Thus, the ecological dynamics of natural selection can be just as complicated for both consumer divergence and convergence.

These same issues also explain why the initial mean trait relationships among the species can push the system to alternative equilibria. The shapes of these fitness surfaces change as the species abundances and trait distributions change in response to one another (McPeck 2017b; a; and see the animation of Fig. 3 in the electronic appendix). Without some intrinsic differences among the species, only the initial trait distributions can cause more than one adaptive peak to exist or make selection move a species from one peak to another. For example, consider the difference between the two parameter combinations represented in Figures 6A and 6B. In Figure 6A, because the intrinsic birth and death optima are all at the same trait value, the only way for the two resources to evolve in different phenotypic directions is for them to begin straddling the consumers' trait means. Thus, the initial trait distributions are the only system feature that provides the impetus for the resources to differentiate. In contrast, initial trait distributions make no difference in Figure 6B because the resources' intrinsic birth optima already straddle the consumers' intrinsic death optima. Here, selection always pulls the resources' phenotypic distributions apart, regardless of where the resources or consumers start. These results and those of previous analyses of these types of models (e.g., Schreiber et al. 2011) highlight that the structure of the final community can be highly contingent on the features of invading species as the community is assembled, because of the contingent nature of natural selection.

In considering the development of community structure, we typically only consider the resource competitive abilities of consumers **after** differentiation has occurred, instead of exploring potential intrinsic differences among consumers that would also foster or retard their differentiation. Consumers may differ in fundamental features of their resource competitive

abilities that limit their scope for evolving in response to the resources, and similarly differences in the fundamental capabilities of the apparent competitive abilities of the resources may also shape how consumers differentiate in response to them. For example, a consumer's resource competitive ability is not simply its ability to acquire a particular resource from the environment, but rather it is the fitness balance between the benefits of feeding on that resource and the costs of other demographic processes (i.e., the denominator and numerator, respectively, of $f_j(z_{N_j}) / (a_j(z_{R_i}, z_{N_j}) b_j)$ in Tilman's (1980; 1982) R^* rule). Before differentiation, one consumer may be a poorer resource competitor on all available resources because these demographic costs are higher for that species but it is in every way identical to its resource competitors in its intrinsic capabilities to utilize the resources (e.g., the scenarios depicted in Fig. 5B). If it could not adapt, this consumer with higher demographic costs (higher f_j) would be driven extinct by resource competition with the consumer having lower demographic costs. Adaptation resulting in differentiation allows the consumer with higher demographic costs to also increase its benefits from feeding and thereby coexist in the community. Differences in other demographic processes that generate direct forms of intraspecific density dependence may be what fosters the evolution of coexisting generalist and specialist feeders, even though those species have identical underlying capacities for feeding on all available resources (Fig. 5D). However, intrinsic differences among consumers in their abilities to acquire all resources (e.g., differences in the maximum attack coefficient) have little effect on the resulting community structure because they have countervailing effects resulting from apparent and resource competition.

One important issue that is beyond the scope of this paper is whether a single species that occupies a stable fitness minimum (e.g., Fig. 2) will differentiate and in so doing diversify to produce two species in one local community. The scenarios I have modeled here represent situations where two ecologically nearly identical consumers come together in a community, for example when Bateson-Dobzhansky-Muller incompatibilities develop in different parts of a consumer's range to generate reproductive isolation (Bateson 1909; Dobzhansky 1937; Muller

1942; Coyne and Orr 2004), and then one invades the range of the other (McPeck 2017b also discusses other biological examples that may create these scenarios). In most cases, consumers that come together when both are at or near a stable fitness minimum will diverge (e.g., Fig. 3), but a limited set of situations do exist where such consumers will converge to the stable fitness minimum (e.g., Fig. 7A). Additionally, a central problem with splitting one species occupying a stable fitness minimum into two—sympatric ecological speciation—is how to generate reproductive isolation in concert with this disruptive selection (Kondrashov and Kondrashov 1999; Berlocher and Feder 2002; Kirkpatrick and Ravigné 2002; Gavrilets 2004; Bolnick and Fitzpatrick 2007). Evolutionary branching analyses in adaptive dynamics approaches to the problem make the assumption that this will occur (Geritz et al. 1998; Doebeli and Dieckmann 2000; de Mazancourt and Dieckmann 2004; Doebeli 2011). The analyses presented here suggest that the ecological component of such sympatric ecological speciation could be driven by resource competition only if the consumer began at a stable fitness minimum and had a trait distribution between those of two resource species onto which it would diversify. However, these two criteria are necessary but not sufficient in all cases to ensure that the process might proceed.

The reciprocity of ecological and evolutionary dynamics in this model illustrates how understanding of community structure cannot be had without understanding how evolution will shape interactions among the species. Inferences about the evolution of community structure cannot be based on ecological arguments about community stability or likely coexistence. Likewise, the adaptation of species cannot be understood in an ecological vacuum that ignores the ecological context in which they exist, the abundances of the species caused by that ecological context, or the ecological dynamics of natural selection generated by various types of direct and indirect species interactions. Fitness is fundamentally an ecological metric, and so a truly predictive evolutionary theory must explicitly incorporate how the abiotic environment and the dynamics of species interactions shape the fitness surfaces that drive natural selection.

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Figure Legends

Figure 1. The community module of two consumers feeding on two resources that is analyzed in this paper. The double-headed arrows represent trophic interactions between the consumers and the resources that underlie the consumers' birth fitness components and the resources' death fitness components, with the $a(z_{R_i}, z_{N_j})$ identifying the attack coefficient associated with each. The arrow pointing towards each resource identifies its birth fitness component underlain by $c(z_{R_i})$, and the arrow pointing away from each consumer identifies its death fitness component underlain by $f(z_{N_j})$. The species identities are color-coded as in the rest of the figures.

Figure 2. An example of the dynamics of phenotypic differentiation of the two resources and one consumer in which the consumer occupies a stable fitness minimum at equilibrium. The columns are the fitness topographies for (A) R_1 (light green), (B) R_2 (dark green), and (C) N_1 (light blue). The top panel in each column is the topography of overall average fitness for the species, the middle panel is the topography for the average birth fitness component, and the bottom panel is the topography of the average death fitness component once the system reaches its abundance and trait mean equilibrium (i.e., graphing the components of equations (6) and (10)). The vertical dashed line in each panel identifies the equilibrium mean trait value for the species. Parameters were as follows: $c_{0i}=3.0$, $d_i=0.02$, $\gamma_i=0.01$, $\tilde{z}_{R_i}^c=25.0$, $G_{z_{R_i}}=E_{z_{R_i}}=0.2$, $a_{0j}=0.5$, $b_j=0.1$, $\beta_j=5.0$, $f_j=0.15$, $g_j=0.0$, $\theta_j=0.01$, $\tilde{z}_{N_j}^f=25.0$, $G_{z_{N_j}}=E_{z_{N_j}}=0.2$.

Figure 3. An example of the dynamics of phenotypic differentiation of the two resources and two consumers in which species at both trophic levels differentiate. The left four columns are the fitness topographies at the abundance and trait equilibrium for (A) R_1 (light green), (B) R_2 (dark green), (C) N_1 (light blue), and (D) N_2 (dark blue). The top, middle, and bottom panel in each column are as in Fig. 2. The vertical dashed line in each panel identifies the equilibrium mean

trait value for the species. Column E shows the real and functional phenotypic distributions for each species at equilibrium (colors as previously specified). Parameters were as follows: $c_{0i}=3.0$, $d_i=0.02$, $\gamma_i=0.01$, $\tilde{z}_{R_i}^c=25.0$, $G_{z_{R_i}}=E_{z_{R_i}}=0.2$, $a_{0j}=0.5$, $b_j=0.1$, $\beta_j=5.0$, $f_j=0.15$, $g_j=0.0$, $\theta_j=0.01$, $\tilde{z}_{N_j}^f=25.0$, $G_{z_{N_j}}=E_{z_{N_j}}=0.2$. A video of the full dynamics of this example can be found in the electronic appendix.

Figure 4. The outcomes of coevolution at different points along parameter gradients that correspond to major environmental gradients of productivity (A-B the resources' intrinsic birth rate maxima), habitat complexity that affects the abilities of consumers to capture resources (C-D the maximum attack coefficients), and stressors of the consumers that affect their death rates (E-F the consumers' intrinsic death rate minima). The equilibrium trait means and population sizes for the four species are presented. Each filled circle identifies the mean trait value (top panel) and population abundance (bottom panel) for that species in the four-species community with the corresponding value of the parameter on the x-axis. In all simulations in this figure, the intrinsic birth rate optimal trait value for the resources ($\tilde{z}_{R_i}^c$) and the intrinsic death rate optimal trait value for the resources ($\tilde{z}_{N_j}^f$) were all 25.0. Symbols and lines for the different species are color-coded as in Figure 3. Parameters were as follows except for the parameter being manipulated in the figure panel: $c_{0i}=3.0$, $d_i=0.02$, $\gamma_i=0.01$, $\tilde{z}_{R_i}^c=25.0$, $G_{z_{R_i}}=E_{z_{R_i}}=0.2$, $a_{0j}=0.5$, $b_j=0.1$, $\beta_j=5.0$, $f_j=0.15$, $g_j=0.0$, $\theta_j=0.01$, $\tilde{z}_{N_j}^f=25.0$, $G_{z_{N_j}}=E_{z_{N_j}}=0.2$.

Figure 5. Equilibrium trait means that result in communities in which (A) the resources have different intrinsic birth maxima (c_{0i}), or the consumers have different (B) intrinsic death minima (f_{0j}), (C) maximum attack coefficients (a_{0j}), or (D) strengths of density dependence in their death rates (g_j). In each panel, the value for one species is held constant (identified above the panel) and value for the other species is manipulated (given on the x-axis). Symbols and lines for the different species are color-coded as in Figure 3. Parameters were as follows except for the parameter being manipulated in the figure panel: $c_{0i}=3.0$, $d_i=0.02$, $\gamma_i=0.01$, $\tilde{z}_{R_i}^c=20.0$, $\tilde{z}_{R_2}^c$

$=30.0$, $G_{z_{R_1}}=0.2$, $E_{z_{R_1}}=4.0$, $a_{0j}=0.5$, $b_j=0.1$, $\beta_j=5.0$, $f_j=0.15$, $g_j=0.0$, $\theta_j=0.01$, $\tilde{z}_{N_j}^f=25.0$,
 $G_{z_{N_j}}=0.2$, $E_{z_{N_j}}=4.0$.

Figure 6. The effects of manipulating the magnitude of environmental phenotypic variance in the consumers on the equilibrium trait means of the four species. In panel A, all four species have the same optimal trait values for their intrinsic demographic rates, and in panel B, the resource intrinsic birth optima straddle the intrinsic death optima of the consumers. Panels C-E show the equilibrium phenotypic distributions for the four species for three different values for the environmental variance component of the consumer's phenotypic distribution from B (as in Fig. 3E), and panels F-H show the average fitness surfaces for the four species at equilibrium in these same situations (as in Fig. 2). Symbols and lines for the different species are color-coded as in Figure 3. Parameters were as follows in all simulations for this figure except for the parameter being manipulated in the figure panels: $c_{0i}=3.0$, $d_i=0.02$, $\gamma_i=0.01$, $G_{z_{R_1}}=0.2$, $a_{0j}=0.5$, $b_j=0.1$, $\beta_j=5.0$, $f_j=0.15$, $g_j=0.0$, $\theta_j=0.01$, $\tilde{z}_{N_j}^f=25.0$, $G_{z_{N_j}}=0.2$. In panel A, $\tilde{z}_{R_1}^c=\tilde{z}_{R_2}^c=25.0$, $E_{z_{R_1}}=0.2$; and in panel B unless otherwise specified, $\tilde{z}_{R_1}^c=20.0$, $\tilde{z}_{R_2}^c=30.0$, $E_{z_{R_1}}=4.0$, $E_{z_{N_j}}=4.0$.

Figure 7. An example of the dynamics of phenotypic differentiation of the two resources and two consumers when the resources' intrinsic birth optimal trait values are much larger than the consumers' intrinsic death optimal trait values. Equilibrium trait means for communities in which the consumers have different levels of environmental phenotypic variance are shown in panel A. Panels B-D show the trait distributions (as in Fig. 3E) for three values of the consumers' environmental variation, and panels E-G show the average fitness surfaces for the four species at equilibrium for the same three values of the consumers' environmental variation. Symbols and lines for the different species are color-coded as in Figure 3. Parameters were as follows except for the parameter being manipulated in the figure panel: $c_{0i}=3.0$, $d_i=0.02$, $\gamma_i=0.01$, $\tilde{z}_{R_1}^c=22.0$, $G_{z_{R_1}}=E_{z_{R_1}}=0.2$, $a_{0j}=0.5$, $b_j=0.1$, $\beta_j=5.0$, $f_j=0.15$, $g_j=0.0$, $\theta_j=0.01$, $\tilde{z}_{N_j}^f=10.0$, $G_{z_{N_j}}=0.2$.

Figure 1.

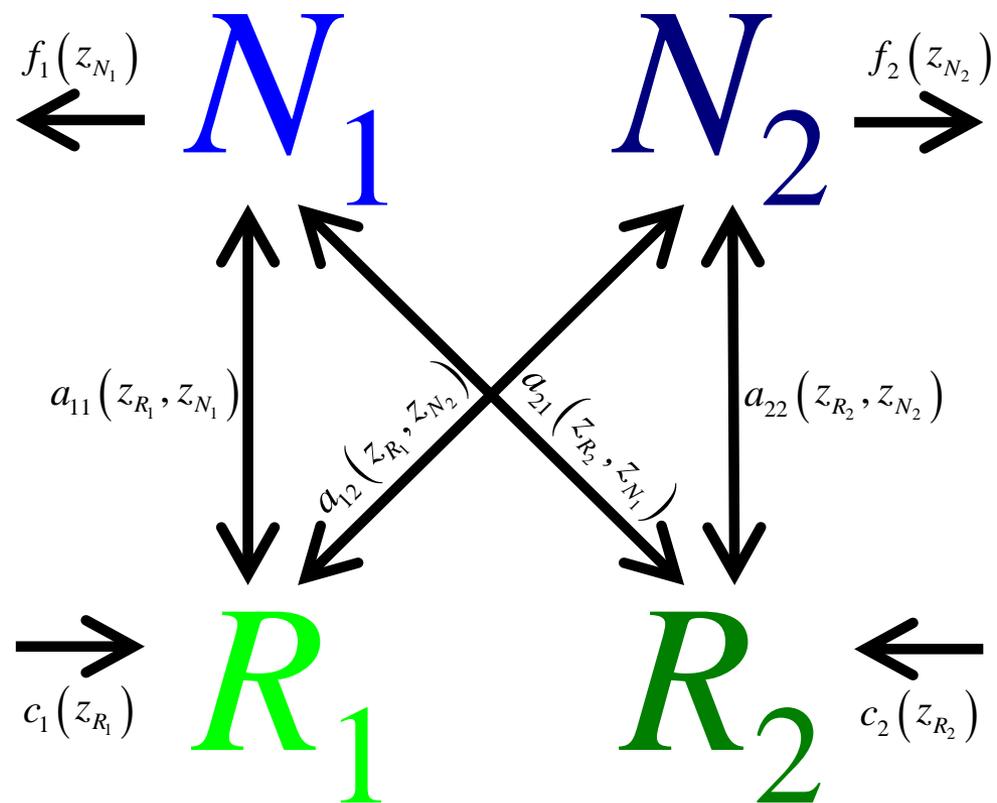


Figure 2.

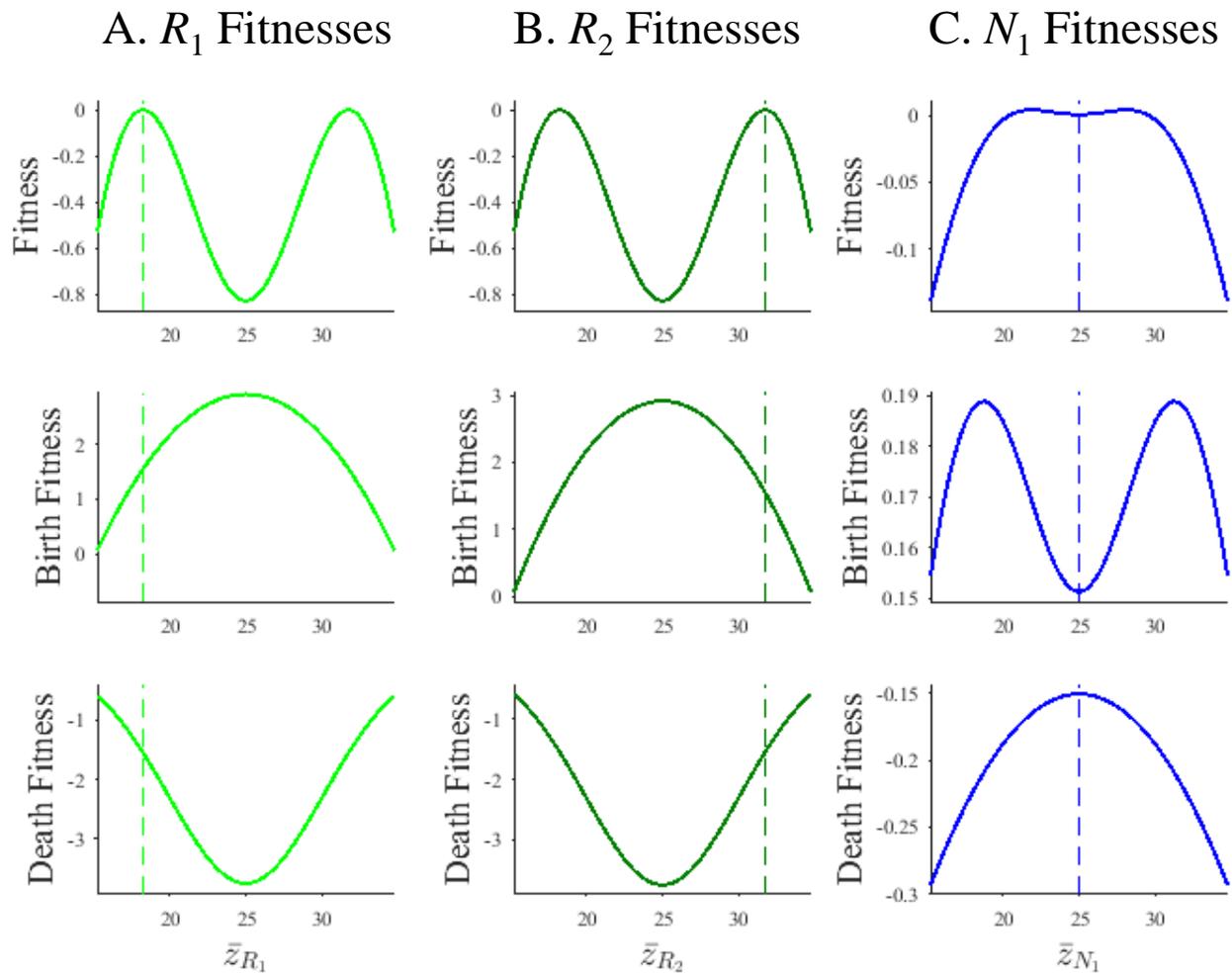
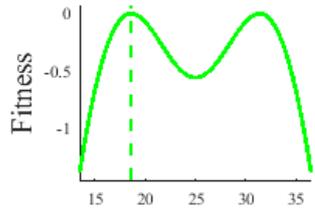
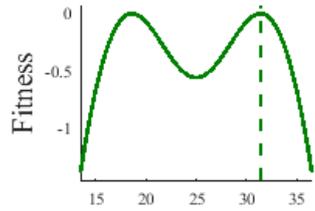


Figure 3.

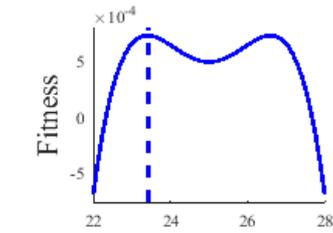
A. R_1 Fitnesses



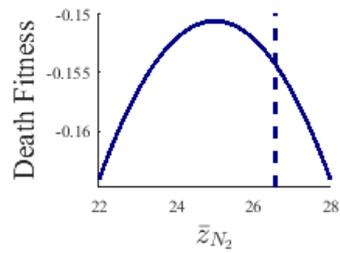
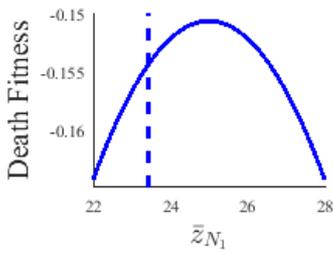
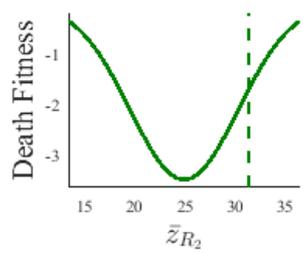
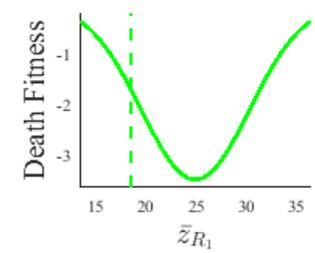
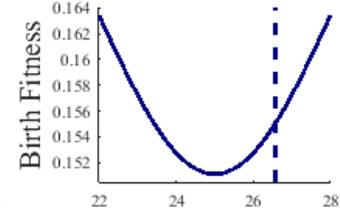
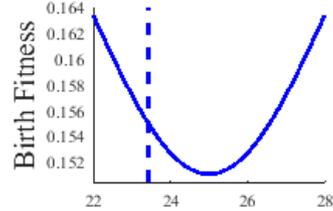
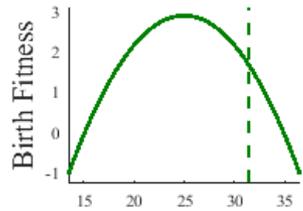
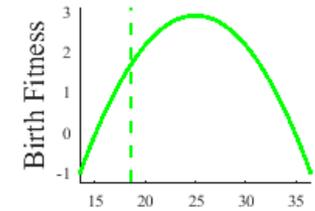
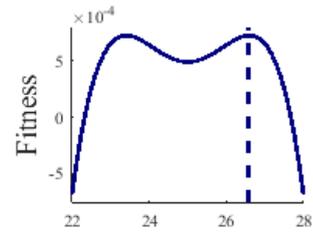
B. R_2 Fitnesses



C. N_1 Fitnesses



D. N_2 Fitnesses



E. Phenotypic Distributions

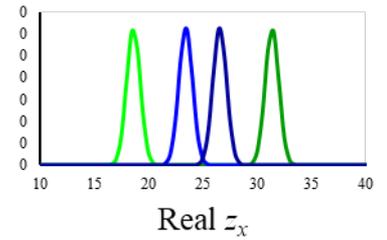
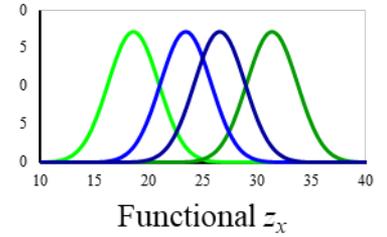


Figure 4.

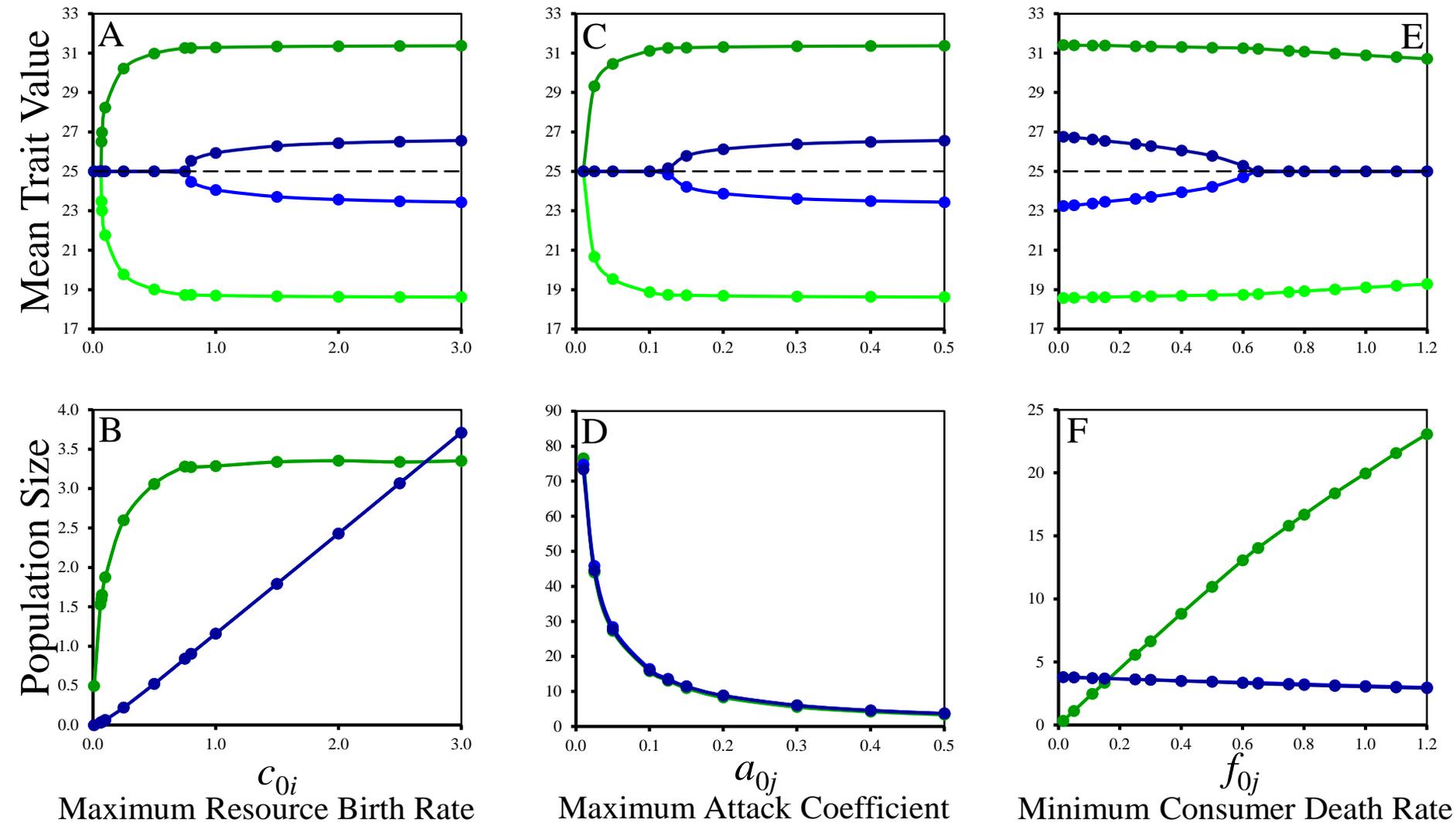
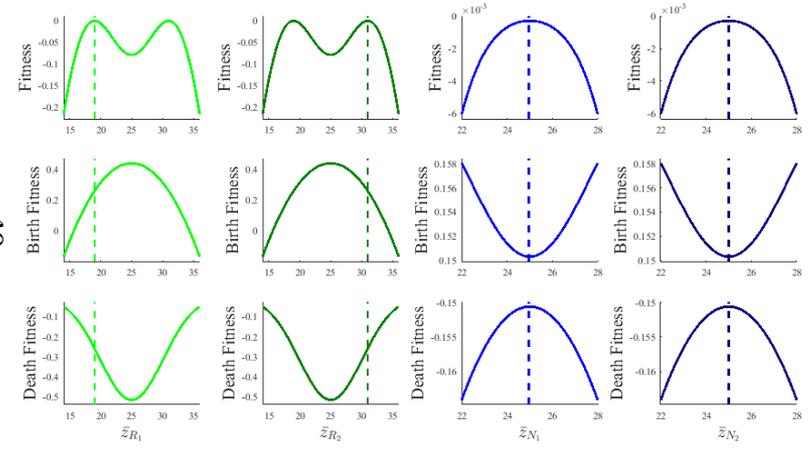


Figure 4 (continued).

G. $c_{0i} = 0.5$



H. $c_{0i} = 3.0$

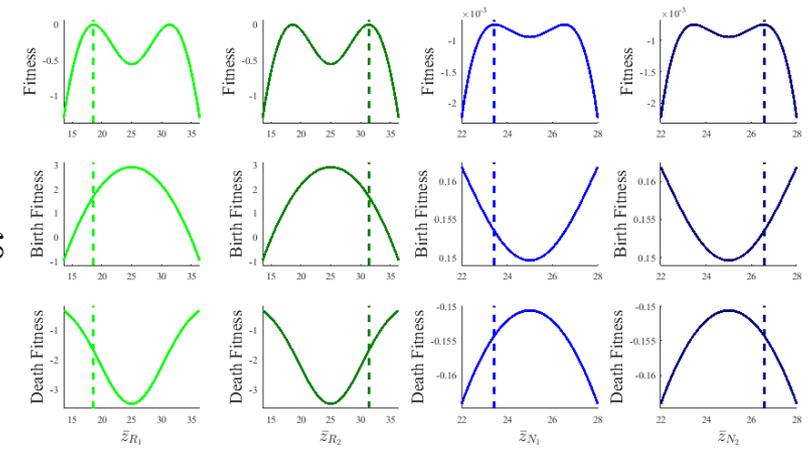


Figure 5.

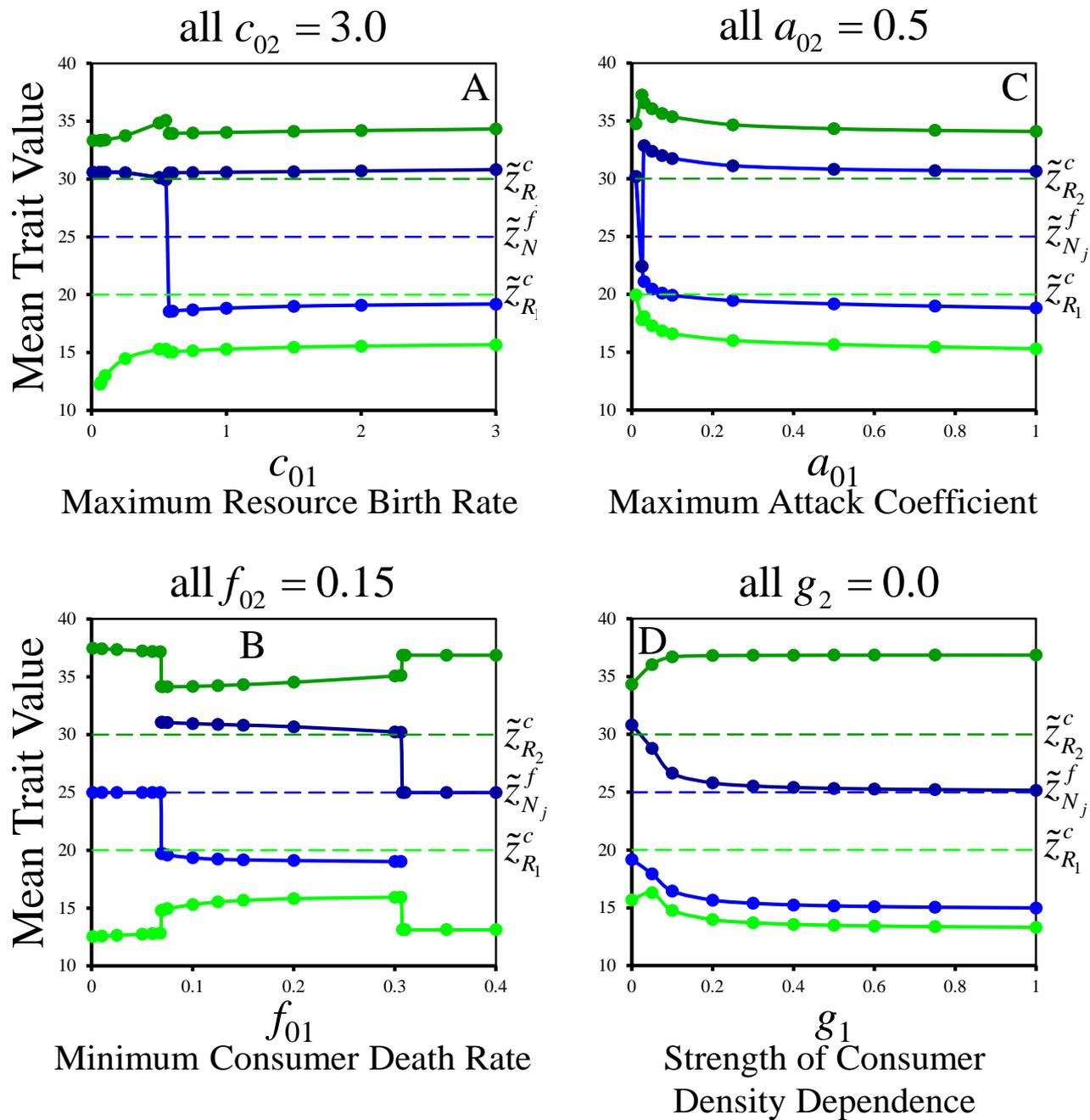


Figure 6.

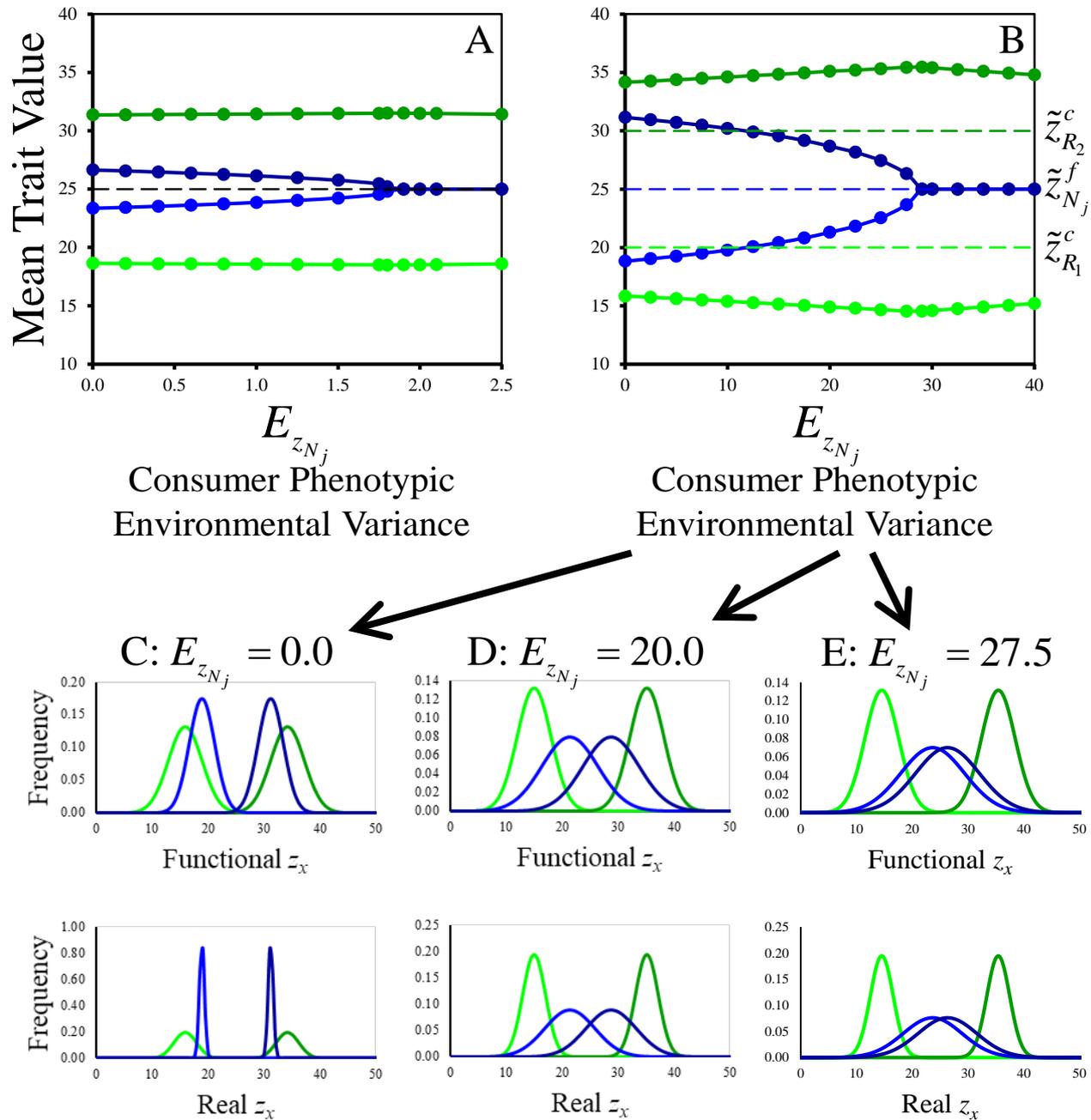


Figure 6 (continued).

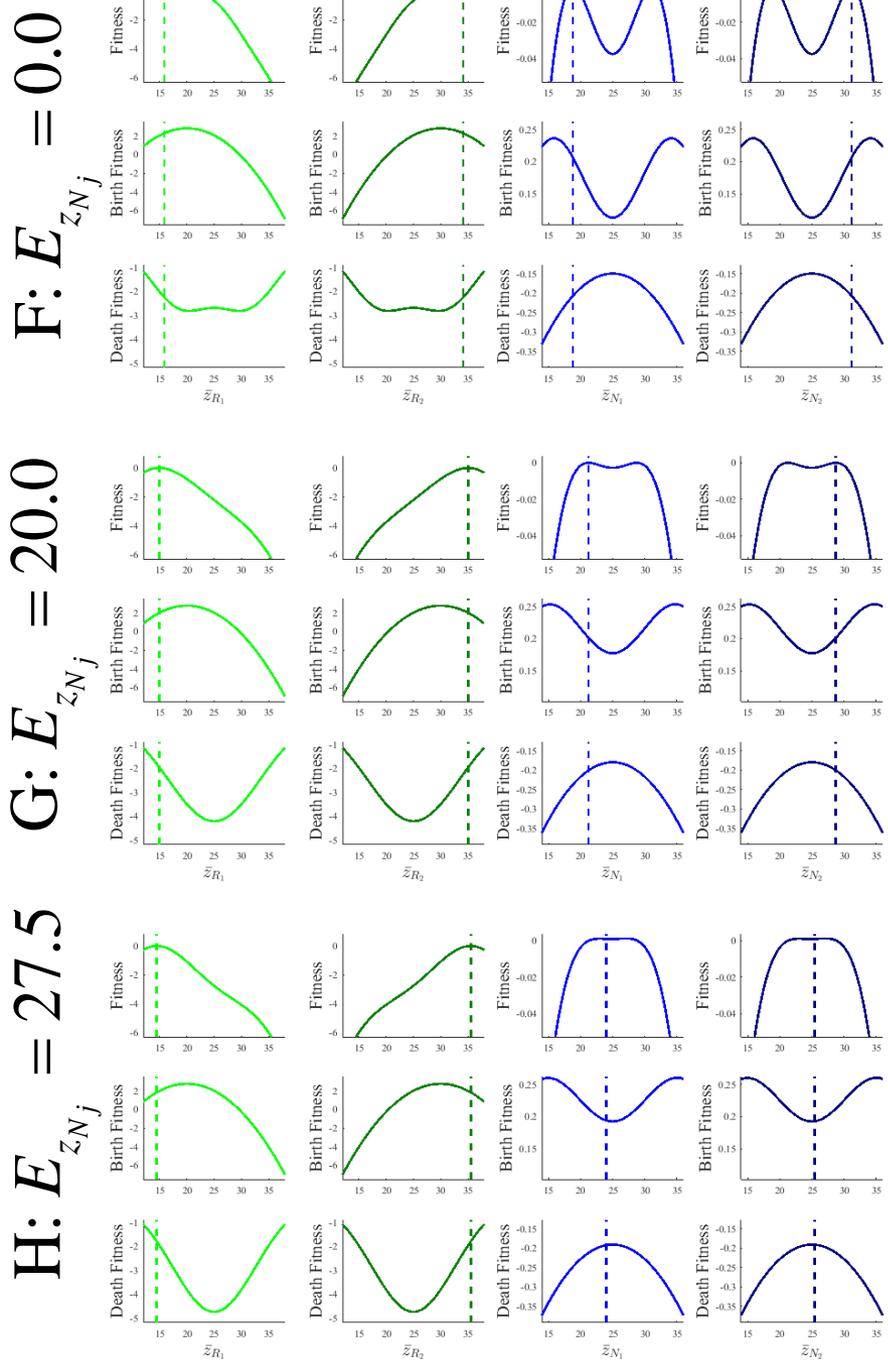


Figure 7.

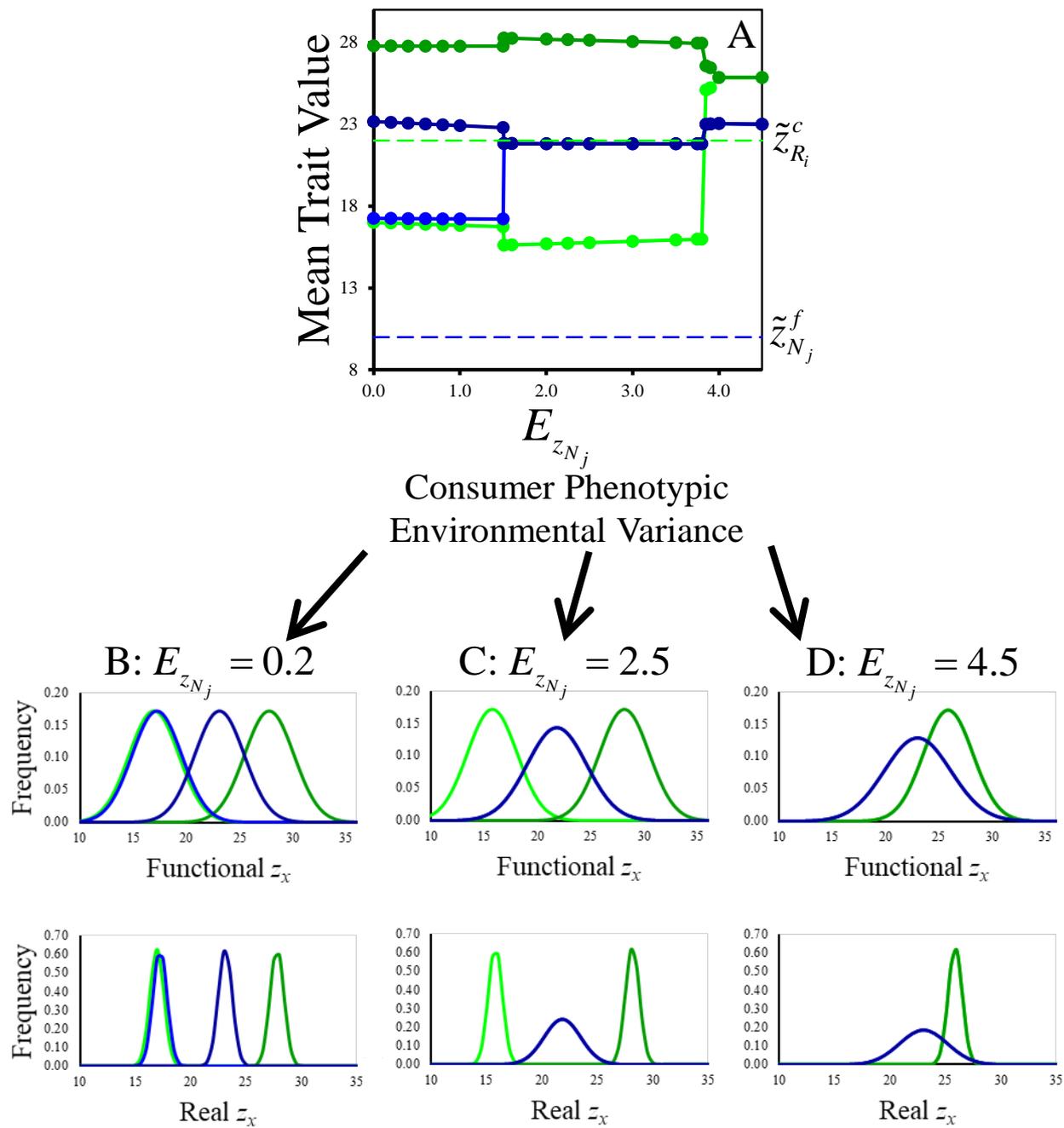
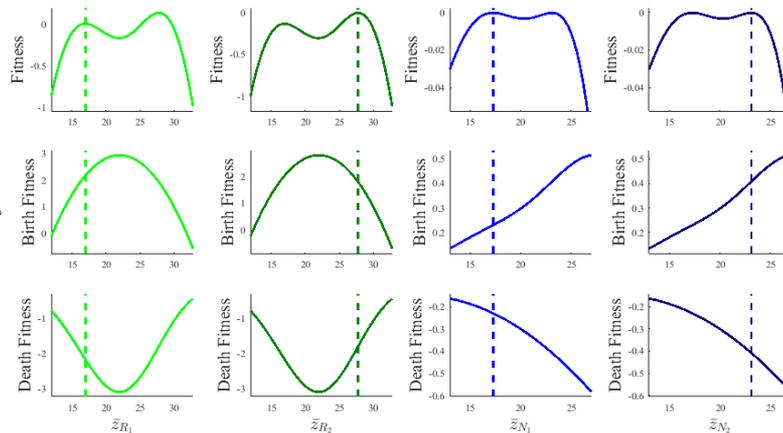
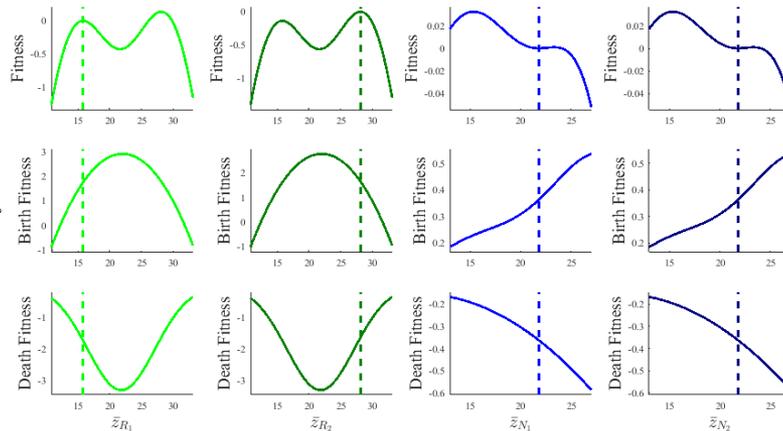


Figure 7 (continued).

E: $E_{z_{N_j}} = 0.2$



F: $E_{z_{N_j}} = 2.5$



G: $E_{z_{N_j}} = 4.5$

