

# Mechanisms influencing the coexistence of multiple consumers and multiple resources: resource and apparent competition

MARK A. MCPEEK<sup>1</sup>

*Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire 03755 USA*

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**Abstract.** Interactions among multiple resources and consumers involve two indirect interactions: resource competition among consumers and apparent competition among resources. However, competition among multiple consumers is typically viewed through the lens of direct interactions embodied in the Lotka-Volterra competition model, which fails to capture the mechanisms of these indirect interactions. In this paper, I analyze various elaborations of MacArthur's and Tilman's original consumer–resource models including more than two species per trophic level, saturating functional responses, and direct intraspecific density dependence within the consumers. First, the simplest model with two resources and two consumers with linear functional responses is analyzed via the structure of the resulting isoclines, and this is reconciled with Tilman's graphical ZNGI/consumption vector approach. With three species at each trophic level even in this simple model, each consumer is not required to have the largest impact on the resource that most limits its growth for multiple consumers to coexist. In fact, a consumer that is an inferior competitor on each resource in isolation may still coexist with superior competitors, and conversely a consumer that is an inferior competitor on each available resource may still be able to drive all other consumers extinct. However, the maximum number of coexisting consumers is set by the number of available resources. Saturating functional responses do not qualitatively alter the conditions for multiple consumers and resources to coexist at a stable point equilibrium but do increase the range of apparent competitive abilities for resources that can invade and coexist. Saturating functional responses also increase the range of dynamics that the community may display (i.e., limit cycles and chaos), which previous analyses have shown can permit more consumer species than resources to coexist. Adding direct intraspecific density dependence in the consumers, either in the form of feeding interference or density-dependent demographic rates, permit more consumers to coexist than available resources, even at stable point equilibria. Understanding the indirect effects that cascade through a community is essential to predicting community changes and understanding how species at multiple trophic levels coexist, and these indirect effects should not be shrouded behind the curtain of Lotka-Volterra competition.

**Key words:** *apparent competition; coexistence; consumer–resource models; indirect effects; intraspecific density dependence; resource competition.*

## INTRODUCTION

No species has their population dynamics defined by a single process. However, community ecologists often presume that only the availability of resources limit species abundances, and so infer that resource competition alone structures communities. Even this is a substantially more complicated presumption than it first appears. Resource competition is by definition an indirect interaction among the species that are consumers of those resources: Each consumer species influences the demography of both itself and its competitors only

indirectly through its effect on resource abundances. If these consumers compete for more than one-resource species, the resources also indirectly interact with one another through their effects on consumer abundances; what Holt (1977) termed “apparent” competition. Despite the rich set of direct and indirect species interactions embedded in this process (Levene 1976), much of our intuition about expected patterns of species coexistence and overall community structure are derived from Lotka-Volterra competition models in which all these indirect interactions are subsumed into direct interactions among the consumer species (e.g., May 1973, Chesson 2000, Adler et al. 2007). Thus, not only do we typically limit our focus to a single type of species interaction, we explore its actions using a model that mischaracterizes how this interaction operates in nature.

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<sup>1</sup> E-mail: mark.mcpeek@dartmouth.edu

The justification for this focus on the Lotka-Volterra competition model as a basis for inquiry is founded on a theoretical transformation. MacArthur (1969, 1970) began with a model of consumer–resource interactions in which all these indirect interactions were explicitly characterized, but he recast all the indirect interactions among these species into the direct interactions of Lotka-Volterra competition among the consumers. To accomplish this, a number of simplifying assumptions were made: Consumer populations are limited only by the amount of resources they harvest; consumers have linear functional responses, equal total harvesting abilities, and equal resource requirements to maintain their populations (or equal demographic rates outside of resource harvesting, depending on how one interprets the meaning of various model parameters); and resource population dynamics are always at equilibrium with respect to current consumer abundances (MacArthur 1969, 1970, 1972). These assumptions make it possible to subsume the consumption of multiple resources into a functional form of the Lotka-Volterra competition coefficient (MacArthur 1969, 1970, 1972, Schoener 1974, Abrams 1975, 1988, Case and Casten 1979, Chesson 1990, Kleinhesselink and Adler 2015, Letten et al. 2017). This approach has also been extended to include the effects of competition and predation (Chesson and Kuang 2008). This was also further generalized to imagine that the consumers feed on a continuous array of many resources along a single axis defined by some phenotypic property of the resource species, and consumers are differentially successful at feeding on resources along this axis (MacArthur and Levins 1967, May and MacArthur 1972, May 1973, 1974, Roughgarden 1974). However, a number of analyses have shown that these assumptions greatly restrict the range of possible community outcomes that can be derived (e.g., Levene 1976, Chesson 1990, Abrams 1998, Abrams et al. 2008, Abrams and Rueffler 2009, Kleinhesselink and Adler 2015). In particular, simplifying assumptions about the resource dynamics completely remove the effects of apparent competition, which greatly distorts the net effect of one consumer on another (Levene 1976, Abrams 1998).

Tilman questioned this approach: “Once such a [consumer–resource] model is formulated, it seems simpler to use the mechanistic model itself, rather than to use it to estimate parameters which are put back into the more descriptive Lotka-Volterra model” (Tilman 1982:6, see also Tilman 1987). In developing his graphical analyses of consumer–resource interactions, Tilman (1980, 1982) utilized various forms of MacArthur’s (1969, 1970, 1972) original consumer–resource model and explored how different types of resources would affect consumer coexistence. His approach explicitly included the population dynamics of both consumers and resources. However, many of these simplifying assumptions (e.g., linear functional responses, equality of various parameters among consumers and among resources, only resource

abundances limit consumer populations) were necessarily maintained to make the analyses graphical. He concluded that no matter the type of resources involved, the number of consumers coexisting locally cannot exceed the number of potentially limiting resources, each coexisting consumer must be limited by a different resource, and each consumer must capture and consume proportionally more of the resource that limits its abundance (Tilman 1980, 1982).

In this paper, I too formally analyze various elaborations of the consumer–resource model originally propounded by MacArthur (1969, 1970, 1972). I begin with a comparable form of his basic model and analyze the criteria for coexistence of multiple consumers with multiple resources in terms of the resource competitive abilities of the consumers and the apparent competitive abilities of the resources. I then relax some of the assumptions made by previous analyses to explore how more realistic forms of the model alter coexistence criteria and the constraints on the resource and apparent competitive abilities of the interacting species. First, when three or more resources are present, the requirements of a specific trade-off in competitive abilities in which each consumer is more limited by the resource on which it is the best resource competitor no longer hold for consumer coexistence. Also, saturating functional responses do not qualitatively alter the criteria for coexistence at a stable point equilibrium, but do permit a greater range of resources to invade and coexist by reducing the restrictions on apparent competitive abilities of resources. More importantly, various forms of direct intraspecific density dependence in the consumers (i.e., feeding interference or density-dependent birth or death rates) permit more consumers to coexist at stable point equilibria than available limiting resources, and saturating functional responses combined with direct consumer intraspecific density dependence enhance the scope for even more consumers to invade and coexist. Matlab code to implement all the models discussed below can be found in the Supporting Information.

#### THE SIMPLEST INTERACTION AMONG MULTIPLE RESOURCES AND CONSUMERS

I start this exploration with the simplest model for multiple consumer species feeding on multiple resource species. The abundance of resource species  $i$  is identified by  $R_i$ , and  $p$  resource species may be present (i.e.,  $i = 1, 2, \dots, p$ ). For present purposes, I will focus on the cases with only two or three resource species present, which allows the exploration of the possibilities of how the consumer guild might deal with alternative resources but maintains simplicity in this exploration. Extrapolation of these results to more than three resources is made by induction. The abundance of consumer species  $j$  is identified by  $N_j$ , and  $q$  consumer species may be present (i.e.,  $j = 1, 2, \dots, q$ ).

Each resource species follows logistic population growth in the absence of any consumers, each consumer

has a linear functional response for feeding on each resource, the consumer's per capita birth rate is determined solely by the quantities of the various resource species it consumes, and each consumer has a density independent death rate. These statements imply the following set of coupled differential equations, which are expressed here in their per capita forms, to describe the abundance dynamics of species inhabiting this community:

$$\begin{aligned}\frac{dR_i}{R_i dt} &= c_i - d_i R_i - \sum_{j=1}^q a_{ij} N_j \\ \frac{dN_j}{N_j dt} &= \sum_{i=1}^p b_{ij} a_{ij} R_i - f_j\end{aligned}\quad (1)$$

In this model,  $c_i$  is the per capita intrinsic birth rate for resource  $i$ , and  $d_i$  scales the rate at which that resource's per capita birth rate declines as its abundance increases. With no consumers, each resource species' abundance equilibrates at  $R_i^* = c_i/d_i$ . The interaction between each pair of consumer and resource species is defined by the attack coefficient,  $a_{ij}$ , the per capita rate at which a consumer  $j$  individual kills and eats resource  $i$  individuals. Each consumer's birth rate is determined by its conversion efficiency,  $b_{ij}$ , of translating eaten resources into consumer offspring. Finally, each consumer species has a per capita intrinsic death rate of  $f_j$ .

This is equivalent to the basic consumer–resource model assumed by MacArthur (1969, 1970, 1972) before being recast into Lotka-Volterra competition and the model considered by Tilman (1980, 1982) for perfectly substitutable resources. As in MacArthur's and Tilman's analyses, each consumer's population growth rate, and consequently abundance, is limited by the quantities of available resources. The density dependence regulating the abundance of each consumer only emerges as indirect effects of their collective depletion of the resources. Thus, the intraspecific and interspecific resource competition that regulates the abundance of each consumer in these models are both indirect effects that are mediated by how consumers deplete resource abundances. Likewise, the intraspecific and interspecific apparent competition that contribute to regulating the abundance of each resource are both indirect effects that are mediated by how resources inflate consumer abundances.

Initially, consider a community module containing two resource species ( $i = 1, 2$ ) and two consumer species ( $j = 1, 2$ ). The equilibrium abundances for this community are found by setting the total growth rate forms of equations in Eq. 1 equal to zero, solving these functions that define the combinations of species abundances at which each population has a population growth rate equal to zero (i.e., the isoclines for the four species) and identifying where these isocline functions intersect (i.e., the points where the species have zero growth rates). In this model, all four isoclines are planes, and their joint intersection at

a single point defines the four-species equilibrium. This equilibrium is feasible if all four species have positive abundances, and this equilibrium can be stable or unstable (Case and Casten 1979, Tilman 1980).

Two criteria must be satisfied for the four-species equilibrium to exist. First, the two consumer isoclines must intersect at positive abundances. Because the per capita population growth rate of each depends only on the abundances of the two resources (Eq. 1), the isocline of each consumer intersects the abundance axes of both resources. These points of intersection with each resource axis occur at  $f_j/(a_{ij}b_{ij})$  for each combination of consumer and resource species (Fig. 1A). In this model,  $f_j/(a_{ij}b_{ij})$  is the equilibrium resource abundance if only resource  $i$  and consumer  $j$  are present, and so the consumer with the lowest value of  $f_j/(a_{ij}b_{ij})$  would drive all other consumers extinct if only this single resource were present. This is a statement of Tilman's "R-star" rule (Tilman 1982). In Fig. 1A,  $N_1$  is a better resource competitor for  $R_1$ , and  $N_2$  is a better resource competitor for  $R_2$ .

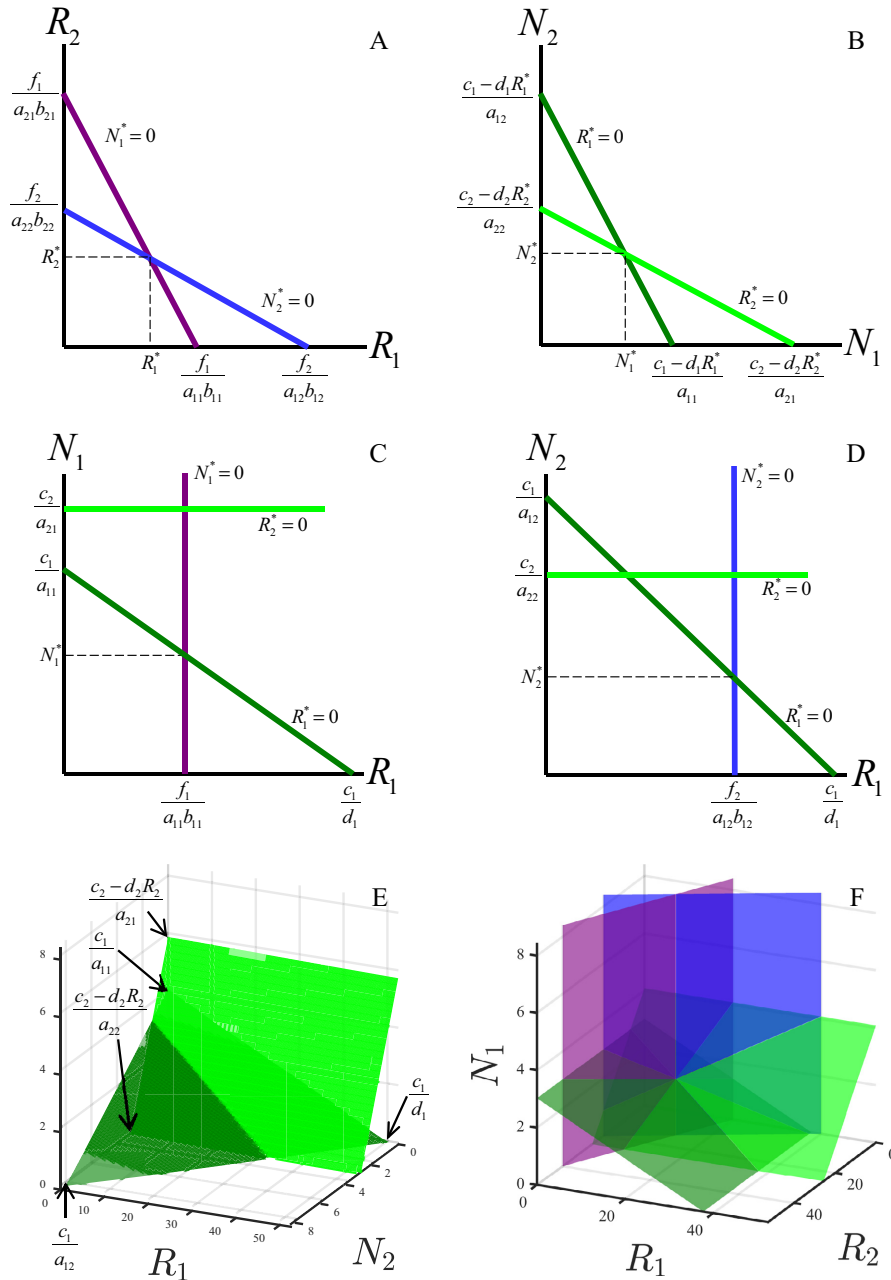
Additionally, because the consumers' per capita population growth rates are independent of their own and the other consumers' abundances (Eq. 1), each consumer isocline runs parallel to both consumer axes (i.e., they do not intersect the consumer axes). Thus, the intersection of the consumer isoclines can be determined by simply evaluating them in the  $R_2$ – $R_1$  face of the state space (i.e., the plane defined by the two resource axes at  $N_1 = N_2 = 0$ ; Fig. 1A). The two consumer isoclines intersect at positive abundances for both resources if

$$\frac{a_{21}b_{21}}{a_{22}b_{22}} < \frac{f_1}{f_2} < \frac{a_{11}b_{11}}{a_{12}b_{12}} \quad (2)$$

is satisfied (Fig. 1A). This inequality demands that, for the two consumers to coexist, each must be a better competitor for a different resource (note that the isoclines could cross in the orientation where  $N_2$  is a better competitor for  $R_1$ , and  $N_1$  is a better competitor for  $R_2$ , but the inequality is satisfied simply by renaming the species). Note the similarity between Fig. 1A and the ZNGI diagrams for perfectly substitutable resources in Figs. 19–22 of Tilman (1982) and Figs. 2–15 of MacArthur (1972). This statement about the requirements for the consumers' isoclines to intersect determines the equilibrium abundances of the resources (Fig. 1A).

This criterion is also what Leibold (1995) identified as the "requirement" component of the consumers' niches, because it states what the consumers require from their environment. However, this criterion is what Leibold (1995) called the "impact" component of the resources' niches, because inequality 2 states the relative impact that the two resources have on their environment, namely the two consumers. Species at one trophic level is "the environment" to species at the other trophic level.

The ability of each resource to exist in the system is defined by its apparent competitive ability in two situations. First, each resource must be able to invade the



community when each consumer is present alone and at equilibrium with the other resource (Holt 1977). For example, consider the community when only  $R_1$  and  $N_1$  are present. They will come to the equilibrium defined by the point of intersection of their isoclines in the  $R_1$ - $N_1$  face (i.e., when  $R_2 = N_2 = 0$ ; Fig. 1C).  $R_2$  can invade and coexist in this community if its isocline intersects the  $N_1$  isocline above the point where  $R_1$ 's isocline intersects the consumer's isocline (Holt 1977). The  $R_2$  isocline runs parallel to the  $R_1$  axis and the  $R_1$  isocline runs parallel to the  $R_2$  axis because the per capita growth rate of each is not directly affected by the other's abundance (Eq. 1).

Because the  $R_2$  isocline is parallel to the  $R_1$  axis in this case, this requires that  $c_2/a_{21} > N_1^*$  in Fig. 1C. Likewise,  $R_2$  must have the analogous relationships to be able to invade the community of  $R_1$  and  $N_2$  (Fig. 1D), and analogous relationships must be true for  $R_1$  invading communities of  $R_2$  at equilibrium with each consumer (figures not shown).

The second important apparent competitive relationship defines the second criterion for two resources and two consumers to coexist at a stable equilibrium: The resource isoclines must intersect at the four-species equilibrium as in Fig. 1B, given the relationships in Figure 1A. The

FIG. 1. Isocline portraits of two resources being fed upon by two consumers, with their dynamics being described by Eq. 1, in which each resource has logistic population growth in the absence of the consumers, the consumers have linear functional responses for feeding on the resources, and neither consumer experiences any intraspecific density dependence. The parameters used in this figure result in a stable four-species equilibrium, with consumer 1 being better at capturing resource 1, and consumer 2 being better at capturing resource 2. The various panels show different vantages on this four-dimensional system. (A) The two-dimensional view of the two consumer isoclines are shown in the subspace of the two resource axes. The isocline for consumer 1 is colored purple, and that for consumer 2 is colored blue. Because the consumer isoclines are both parallel to both consumer axes, these isoclines have this identical relationship for all values of consumer abundances. Their intersection point defines the equilibrium abundances of the two resources (i.e.,  $(R_1^*, R_2^*)$ ). (B) The two-dimensional view of the two resource isoclines are shown in the subspace of the two consumer axes. The isocline for resource 1 is colored dark green, and that for resource 2 is colored light green. The positions of these isoclines in this subspace change with the abundances of the two consumers. If these two isoclines intersect when the resources are at their equilibrium abundances (as shown here), their intersection point defines the equilibrium abundances of the two consumers (i.e.,  $(N_1^*, N_2^*)$ ). (C and D) Illustrations of the necessary relationships between the positions of the isoclines for  $R_2$  to be able to invade communities of (C) only  $R_1$  and  $N_1$  and (D) only  $R_1$  and  $N_2$ . In each,  $N_1^*$  identifies the equilibrium abundance of that consumer when only  $R_1$  is present. (E) The two resource isoclines are shown in the  $R_1$ – $N_2$ – $N_1$  subspace to illustrate why the positions of these isoclines change in panel B as the resource abundances change. (F) The isoclines of all four species are shown in the  $R_1$ – $R_2$ – $N_1$  subspace when  $N_2 = N_2^*$  to illustrate the relationships among the isoclines when a stable four-species equilibrium exists. In panels E and F, the origin of the axis system is at the intersection point of the three faces in the back corner. The parameter values used for this figure are  $c_1 = c_2 = 2.0$ ,  $d_1 = d_2 = 0.04$ ,  $b_{11} = b_{12} = b_{21} = b_{22} = 0.1$ ,  $f_1 = f_2 = 1.0$ ,  $a_{11} = a_{22} = 0.5$ , and  $a_{21} = a_{12} = 0.25$ .

positions of the two resource isoclines on the consumer axes in two-dimensional (2D) space depend on their own abundances as well (i.e., the 2D representation presented in Fig. 1B is a slice through the full 4D state space of this system at  $[R_1^*, R_2^*]$  (the point identifying the equilibrium abundances of the two resources at the four-species equilibrium) on the axes not depicted). The positions of the resource isoclines in Fig. 1B define  $R_2$  as a better apparent competitor against  $N_1$  at the four-species equilibrium (i.e.,  $(c_2 - d_2 R_2^*)/a_{21} > (c_1 - d_1 R_1^*)/a_{11}$  where the equilibrium resource abundances here are the values at the four-species equilibrium), and  $R_1$  is a better apparent competitor against  $N_2$  at the four-species equilibrium (i.e.,  $(c_1 - d_1 R_1^*)/a_{12} > (c_2 - d_2 R_2^*)/a_{22}$  (Holt 1977). These differences in the apparent competitive abilities of the two resources at equilibrium are essential for all four species to coexist, because they assure that the resource isoclines intersect at positive abundances.

The relationship between the resource isoclines when they are at their equilibrium abundances (i.e., Fig. 1B) also defines an inequality that states the relative effects of each consumer on the two resources for coexistence, given the relationship in inequality 2:

$$\frac{a_{12}}{a_{22}} < \frac{c_1 - d_1 R_1^*}{c_2 - d_2 R_2^*} < \frac{a_{11}}{a_{21}}. \quad (3)$$

This criterion is equivalent to the supply point of the two resources being within the wedge formed by the consumption vectors in Tilman's graphical presentation (MacArthur 1972, Tilman 1980, 1982, Petraitis 1989). To see why, consider the 3D  $N_1$ – $N_2$ – $R_1$  representation of the four isoclines depicted in Fig. 2. The panels in the right column of Fig. 2 show the isoclines when  $R_2$  is held constant at various abundances and the other species are at their equilibrium abundances given the fixed abundance of  $R_2$ . As  $R_2$  is increased, its isocline moves closer to the  $N_1$ – $R_1$  face, because its intersection points with the  $N_1$  and  $N_2$  axes move toward the origin (Fig. 1E).

Consequently, the intersection line between the two resource isoclines moves. Furthermore, the two consumer planes move toward the origin along the  $R_1$  axis with increasing values of  $R_2$  (see panels in the right column going up in Fig. 2). Because of their resource competitive relationships,  $N_2$ 's isocline intersects the  $R_1$  axis above that of  $N_1$  when  $R_2$  is at low abundance, but moves faster toward the origin and eventually passes the  $N_1$  isocline as  $R_2$  is increased. The two consumer isoclines are coincident in this view when  $R_2$  is at its own equilibrium abundance (the middle panel in the right column of Fig. 2). (Analogous relationships are apparent if the  $N_1$ – $N_2$ – $R_2$  representation along a gradient of  $R_1$  abundances is considered.) Inequality 3 ensures that the consumer isoclines are coincident at a point where they also still cross the line of intersection between the resource isoclines. (See McPeck [2014, 2017b] for analogous considerations of competing consumers in diamond and intraguild predation community modules.)

Inequality 3 also states the “impact” niche components for the consumers and the “requirement” niche components for the resources (Leibold 1995). As a final vantage on this system, Fig. 1F shows all four isoclines in the  $N_1$ – $R_1$ – $R_2$  3D space when the species are all at their stable equilibrium abundances.

If the ratio of resource productivities at equilibrium is outside the range defined by the attack coefficient ratios (i.e., inequality 3 not satisfied), the two consumer isoclines will be coincident at a point where they do not intersect the line of intersection between the resource isoclines. If the  $R_2$  isocline moves toward the origin too quickly with increasing  $R_2$ , the line of intersection of the resource isoclines could end at a higher  $R_1$  than the coincidence point of the consumer isoclines (Fig. 3A). In this case, only  $N_1$  would coexist with the two resources, because it decreases the combined resource abundances below a point at which  $N_2$  can persist. One can project this situation as a statement about the resource competitive abilities of the two consumers. However, this

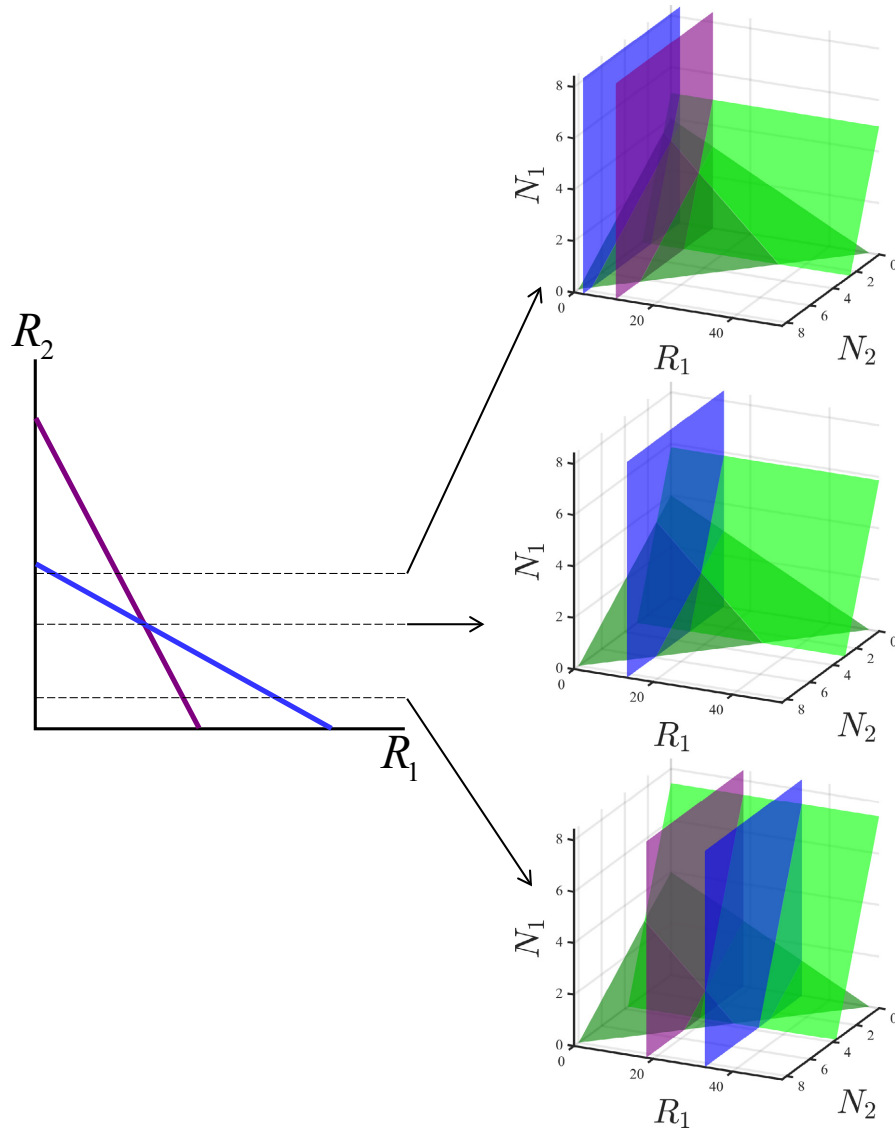


FIG. 2. Various representations of the isocline system defined by Eq. 1 to illustrate the relationship between (the right column of panels) positions of all four species in the  $R_1$ – $N_2$ – $N_1$  subspace relative to the two-dimensional view illustrated in Fig. 1A. As the abundance of resource 2 is changed (i.e., moving along the  $R_2$  axis in Fig. 1A), the positions of all four isoclines change in the three-dimensional subspace. The isoclines are colored as in Fig. 1. At a value of  $R_2$  below  $R_2^*$  (e.g., the lower dashed line in the two-dimensional panel), the isocline plane for consumer 1 is at a lower value of  $R_1$  axis than consumer 2's isocline. When  $R_2 = R_2^*$  (middle dashed line), the two consumer isoclines are coincident at the same point on the  $R_1$  axis. At a value of  $R_2$  above  $R_2^*$  (e.g., the upper dashed line in the two-dimensional panel), the isocline plane for consumer 2 is at a lower value of  $R_1$  axis than consumer 1's isocline. In the three-dimensional panels, the origin of the axis system is at the intersection point of the three faces in the back corner. Parameters are as given in Fig. 1.

situation is actually defined by the apparent competitive abilities of the two resources. Note that when the two consumers isoclines are coincident in Fig. 3A, the  $R_1$  isocline intersects the two consumer isoclines above the  $R_2$  isocline. In this case,  $R_1$  is productive enough to inflate  $N_1$ 's abundance and thereby depress the abundance of  $R_2$  to the point where  $N_2$  cannot invade and persist with its preferred resource (remember that here I am considering the situation of resource competitive

abilities defined in Fig. 1A). Conversely, the consumer isoclines may be coincident at a higher  $R_1$  value before they reach the resource isocline intersection (Fig. 3B); in this case, only  $N_2$  would coexist with the two resources. Again, this results from  $R_2$  being more productive and thus inflating the abundance of  $N_2$  to the point where  $N_1$  cannot invade the community. These represent situations analogous to the supply points being outside the consumption vector wedge in Tilman's graphical

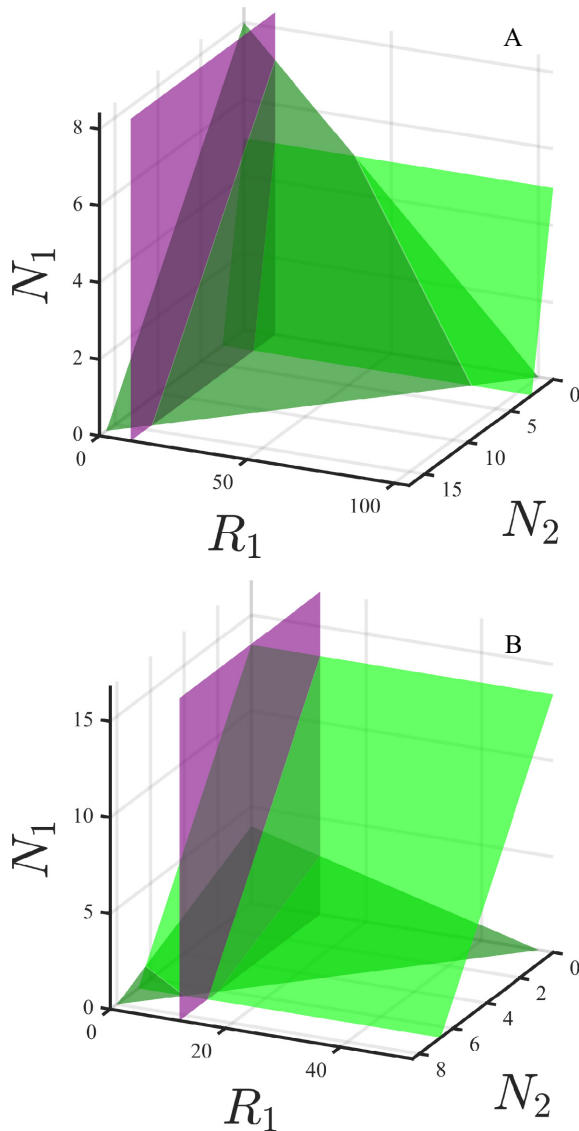


FIG. 3. Alternative parameter combinations where only one consumer can coexist at a stable equilibrium with two resources for Eq. 1. The isoclines are colored as in Fig. 1 and all parameter values are as given in Fig. 1 unless otherwise specified. Each panel illustrates the point where the two consumer isoclines are coincident on the  $R_1$  axis to show that at this point they do not cross the intersection between the two resource isoclines, which is required for the four-species equilibrium. (A) Resource 1 has a higher intrinsic birth rate than resource 2 ( $c_1 = 4.0$ ,  $c_2 = 2.0$ ), and so only consumer 1 can coexist with the two resources. (B) Resource 2 has a higher intrinsic birth rate than resource 1 ( $c_1 = 2.0$ ,  $c_2 = 4.0$ ), and so only consumer 2 can coexist with the two resources. In the three-dimensional panels, the origin of the axis system is at the intersection point of the three faces in the back corner.

representation (MacArthur 1972, Tilman 1980, 1982). Thus, two consumers cannot coexist when the supply point is outside of the wedge created by their consumption vectors (e.g., Fig. 24 of Tilman 1982) because of the relative apparent competitive abilities of the two

resources and not because of the relative resource competitive abilities of the two consumers.

Alternatively, if the resource isoclines were reversed in their relationships in Fig. 1B but the relationships in Fig. 1A hold:  $R_2$  is the better apparent competitor against  $N_2$ , and  $N_2$  is the better resource competitor on  $R_2$ ; but  $R_1$  is the better apparent competitor against  $N_1$ , and  $N_1$  is the better resource competitor on  $R_1$ ; the four-species equilibrium is unstable, and only one consumer will coexist with the two resources depending on initial conditions (Tilman 1980, 1982). Thus, stable coexistence in this case requires specific relationships between the resource competitive abilities of the consumers and the apparent competitive abilities of the resources.

With only two resources, at most two consumers can coexist in this model. A third consumer could possibly coexist only in the trivial case of its isocline also passing through the point of intersection of  $N_1$  and  $N_2$ 's isoclines, which is exceedingly unlikely.

#### ADDING MORE RESOURCES AND MORE CONSUMERS

More generally, the maximum number of coexisting consumer species is equal to the number of available resource species for model 1 (Tilman 1980, 1982). The relationship between the consumer isoclines in Fig. 1A implies a trade-off in their resource competitive abilities where coexistence requires that each consumer is more limited by the resource that it is better able to capture and consume (Tilman 1982). This trade-off is the basis for inference from the ZNGI/consumption vector approach to understanding this interaction (Tilman 1980, 1982, Letten et al. 2017). One might think to extend this implication by inference to situations when more than two consumer and two resources are present: that would be wrong.

Fig. 4 shows the resource and consumer isoclines in the appropriate 3D spaces for four different parameter combinations of three consumers feeding on three resources. Remember that the consumer isoclines are independent of the resource axes, and the resource isoclines are independent of the consumer axes for model 1. In Fig. 4A, each consumer is the best competitor on a different resource, and all three consumers coexist at a stable equilibrium, which is consistent with extrapolating the results from two resources and two consumers to the multiple of each. In this case, a six-species stable equilibrium exists. This point is identified where all the intersection lines between pairs of consumer isoclines themselves intersect at a single point, where all the intersection lines between pairs of resource isoclines themselves intersect at a single point (Fig. 4A), and where all three consumer isoclines are coincident within the intersection of the three resource isoclines. Numerical simulations demonstrate that this six-species equilibrium is stable.

Fig. 4B again shows an isocline configuration in which each consumer is the best competitor on a different resource. For this parameter set, the intersection lines do

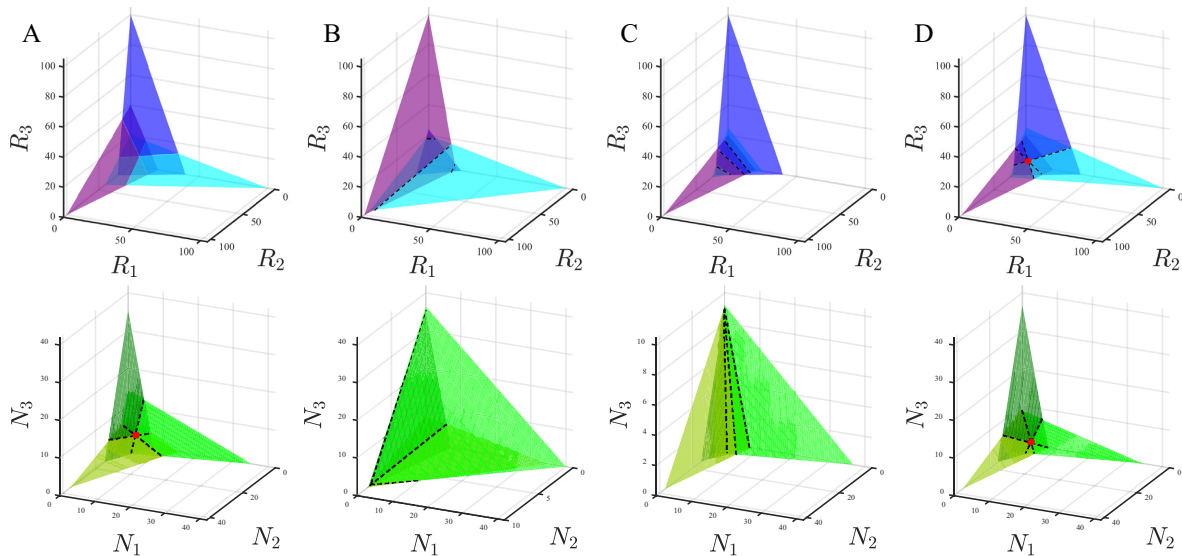


FIG. 4. Consumer and resource isocline portraits in the three-dimensional resource space when three consumers feed on three resources for alternative parameter combinations of Eq. 1. The top panel in each shows the three consumer isoclines in  $R_1$ – $R_2$ – $R_3$  subspace. The  $N_1$  isocline is purple, the  $N_2$  isocline is dark blue, and the  $N_3$  isocline is light blue. The bottom panel in each shows the three resource isoclines in  $N_1$ – $N_2$ – $N_3$  subspace. The  $R_1$  isocline is in dark green, the  $R_2$  isocline is in light green, and the  $R_3$  isocline is in yellow green. In each pair of panels, the dashed lines identify the lines of intersection between pairs of isoclines, and the red circle identifies the stable equilibrium point if one exists. The parameter values that are common to all panels are  $c_1 = c_2 = c_3 = 4.0$ ,  $d_1 = d_2 = d_3 = 0.04$ ,  $b_{11} = b_{12} = b_{13} = b_{21} = b_{22} = b_{23} = b_{31} = b_{32} = b_{33} = 0.1$ , and  $f_1 = f_2 = f_3 = 1.0$ . The parameters that differ among the panels are as follows: (A)  $a_{11} = a_{22} = a_{33} = 0.5$ ,  $a_{13} = a_{21} = a_{32} = 0.1$ , and  $a_{12} = a_{23} = a_{31} = 0.25$ ; (B)  $a_{11} = a_{22} = a_{33} = 0.5$ ,  $a_{13} = a_{21} = a_{31} = 0.1$ ,  $a_{12} = a_{32} = 0.42$ , and  $a_{23} = 0.11$ ; (C)  $a_{11} = a_{22} = a_{31} = 0.5$ ,  $a_{21} = a_{32} = 0.1$ ,  $a_{13} = a_{23} = a_{33} = 0.4$ , and  $a_{12} = 0.25$ ; and (D)  $a_{11} = a_{22} = a_{31} = 0.5$ ,  $a_{21} = a_{32} = a_{13} = 0.1$ ,  $a_{23} = a_{33} = 0.4$ , and  $a_{12} = 0.25$ .

not themselves intersect at a single point for either the resource or consumer isoclines perspectives (Fig. 4B). In this case,  $N_2$  drives the other two consumers extinct to feed exclusively on  $R_1$  and  $R_3$  at equilibrium:  $R_1$  and  $R_3$  inflate  $N_2$ 's abundance to a level that drives  $R_2$  extinct. This three-species equilibrium is stable. Just as when two resources and two consumers are present, the mere fact that each consumer is the best competitor on one of the available resources does not ensure that all the consumers will be present in the community.

However, unlike with two resources and two consumers, a consumer does not need to be the best competitor on any available resource to be a member of the community when three or more resource species are present. In Fig. 4C,  $N_1$  is the superior competitor on two resources,  $N_2$  is superior on the third, and  $N_3$  is a subordinate competitor on all three available resources. Again, the intersection lines of the consumer isoclines do not themselves intersect (Fig. 4C), and so the three consumers cannot coexist with one another. Remember that the intersection of the resource isoclines set the consumer equilibrium abundance, and here they intersect at  $[N_1, N_2, N_3] = [0, 0, N_3^*]$ .  $N_3$  is a subordinate resource competitor on all three resources but drives the other two consumers extinct to feed alone on the three available resources at a stable equilibrium. Even though  $N_3$  would be driven extinct by one of the other consumers if only

one resource was available, it depresses the combined abundances of the three resources to levels at which the other two consumers cannot maintain a population.

Finally in Fig. 4D,  $N_1$  is again the superior competitor on two resources,  $N_2$  is superior on the third, and  $N_3$  is again the superior competitor on none of the available resources (in fact, the only difference from Fig. 4C is the competitive ability of  $N_3$  on  $R_1$ ), but in this case, all three consumers coexist on the three resources at a stable equilibrium. Here, all three consumers derive most of their nutrition from only two of the three resources (i.e., each consumer has one value of  $f_i/(a_{ij}, b_{ij})$  that is substantially larger than the other two), one is an inferior competitor on all available resources, and another is the best resource competitor on two resources.

Thus, no general relationships among resource competitive abilities will ensure the presence or absence of any consumer in the system if more than two resource species are available. This also implies that with more than two resources, no single specific trade-off structure in competitive ability is required among the consumers for their coexistence. For example, Fig. 4A illustrates a community in which the consumers are each most limited by the resource on which they are the best competitor: the trade-off inferred from Tilman's (1980, 1982) analyses with two resources. However, coexistence of the three consumers in Fig. 4D illustrates what one might consider a generalist/

specialist trade-off in which  $N_3$  is a generalist that is relatively good at feeding on two of the resources but not the best on either, whereas the other two consumers are each the best resource competitor on different resources. These may not be the only configurations of species properties that permit coexistence of three consumers feeding on three resources, and an even greater variety of trade-off structures may permit consumer coexistence when more than three resources are available. As of now, no single statement can be made about the apparent competitive abilities of the resources to ensure their presence or the presence of specific consumers in the community if three or more resources may be present.

#### ADDING SATURATING FUNCTIONAL RESPONSES

Consumers cannot indefinitely maintain a linearly increasing resource consumption rate with increasing resource abundances. Per capita feeding rates eventually asymptote at high resource abundances, meaning that a saturating rather than a linear functional response is more realistic for resource consumption (Holling 1959). Substituting saturating functional responses (Holling 1959) into Eq. 1 results in a version of the classic Rosenzweig and MacArthur (1963) consumer–resource interaction model for multiple species at each trophic level

$$\begin{aligned} \frac{dR_i}{dt} &= c_i - d_i R_i - \left( \sum_{j=1}^q \frac{a_{ij} N_j}{1 + \sum_{i=1}^p a_{ij} h_{ij} R_i} \right) \\ \frac{dN_j}{dt} &= \frac{\sum_{i=1}^p b_{ij} a_{ij} R_i}{1 + \sum_{i=1}^p a_{ij} h_{ij} R_i} - f_j \end{aligned} \quad (4)$$

where  $h_{ij}$  is the handling time of consumer  $j$  feeding on resource  $i$ , and all other parameters are as described for Eq. 1.

Previous analyses have shown that saturating functional responses open the possibility of more consumers coexisting than available resources if some of the consumers display limit cycles or chaotic dynamics (Zicarelli 1975, Armstrong and McGehee 1976, 1980, McGehee and Armstrong 1977, Huisman and Weissing 1999). While holding this more general dynamical result in mind, I want to focus in this section on how saturating functional responses change the shapes of and relationships among the isoclines of consumers and resources and what these changes imply about the ecological abilities of those coexisting species.

The consumer isoclines change in their quantitative positions on the axes but remain planes that are parallel to both consumer axes; each intersects each resource axis at  $f_j/(a_{ij}(b_{ij}-f_j h_{ij}))$  (Fig. 5B,C). The relative competitive abilities of the various consumers for each specific resource are also still ordered according to where they intersect that

resource's axis. The consumer with the lowest  $f_j/(a_{ij}(b_{ij}-f_j h_{ij}))$  on a given resource is still able to drive all other consumers extinct if only that resource is present in the community and no species displays cyclical or chaotic population dynamics (Fig. 5C) (McPeck 2012). However, the resources will equilibrate at higher abundances with larger handling times. Also, inequality 2 is more elaborate, but qualitatively similar

$$\frac{a_{21}(b_{21}-f_1 h_{21})}{a_{22}(b_{22}-f_2 h_{22})} < \frac{f_1}{f_2} < \frac{a_{11}(b_{11}-f_1 h_{11})}{a_{12}(b_{12}-f_2 h_{12})} \quad (5)$$

Each resource isocline still intersects consumer  $j$ 's axis at  $c_j/a_{ij}$ , intersects its own axis at  $c_j/d_i$ , and does not intersect any other resource's axis. However, saturating functional responses cause two qualitative changes in the shape of the resource isoclines. First, the resource isocline becomes concave above from its own axis and in the direction of increasing predator abundance with  $h_{ij} > 0$ , and this concavity becomes more pronounced with larger values of  $h_{ij}$  (e.g., note that the  $R_1$  isocline is concave in each of the  $N_1-R_1$  and  $N_2-R_1$  faces in Fig. 5A; Rosenzweig 1969, 1971). Also, instead of running parallel to the axis of the other resource as it did with  $h_{ij} = 0$  (Fig. 1), each resource's isocline increases linearly along the other resource's axis at higher abundances of the other resource. For example, this increase for  $R_2$  in the  $N_1-R_1$  face has slope of  $c_2 a_{11} h_{11}/a_{21}$ : This slope increases with increasing handling time for the other resource (Fig. 5E). The higher abundance of the alternative resource satiates the consumer and thus permits a positive population growth rate for the resource at higher consumer abundances.

Identifying the attack function as  $\hat{a}_{ij} = a_{ij}/(1 + a_{1j} h_{1j} + a_{2j} h_{2j})$ , we can see that although the shapes of the resource isoclines have changed (Fig. 5), and so the positions of the resource equilibrium abundances have changed, inequality 3 defining the existence of the four-species equilibrium does not change

$$\begin{aligned} \frac{\hat{a}_{12}}{\hat{a}_{22}} &< \frac{c_1 - d_1 R_1^*}{c_2 - d_2 R_2^*} < \frac{\hat{a}_{11}}{\hat{a}_{21}} \\ \frac{a_{12}/(1 + a_{12} h_{12} + a_{22} h_{22})}{a_{22}/(1 + a_{12} h_{12} + a_{22} h_{22})} &< \frac{c_1 - d_1 R_1^*}{c_2 - d_2 R_2^*} \\ &< \frac{a_{11}/(1 + a_{11} h_{11} + a_{21} h_{21})}{a_{21}/(1 + a_{11} h_{11} + a_{21} h_{21})} \\ \frac{a_{12}}{a_{22}} &< \frac{c_1 - d_1 R_1^*}{c_2 - d_2 R_2^*} < \frac{a_{11}}{a_{21}} \end{aligned} \quad (6)$$

(Fig. 5D). However, the changes in the resources' isoclines do affect the resources' abilities to invade and establish in the community by altering the apparent competitive abilities of the resources. With all  $h_{ij} = 0$ , each resource can only invade a food chain consisting of the other resource and one consumer (remember two consumers cannot coexist on one resource in model 1) if  $c_i/a_{ij} > N_j^*$  where  $N_j^*$  is the equilibrium abundance of

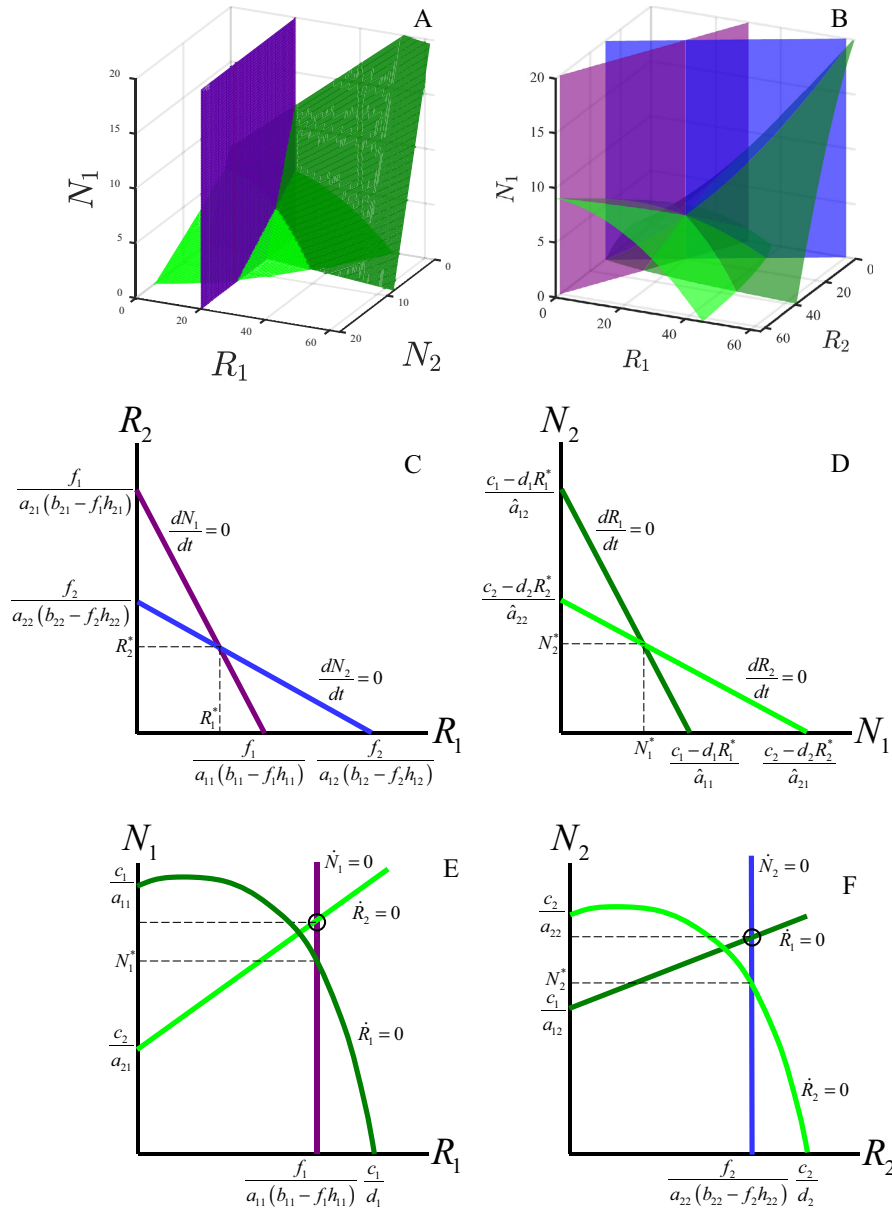


FIG. 5. Isocline portraits in two three-dimensional subspaces when a four-species equilibrium exists and the consumers have saturating functional responses as defined in Eq. 4. (A) The four isoclines are shown in the  $R_1$ - $N_2$ - $N_1$  subspace. Note that the position of resource 2's isocline (light green) on the  $N_1$  axis increases as the abundance of  $R_1$  increases. Also, note the "hump" in resource 1's isocline (dark green) because of the saturating functional response. Because this figure illustrates the four species at equilibrium, the two consumer isocline planes are coincident in panel A (see Fig. 2). (B) The same four-species system is viewed in the  $R_1$ - $R_2$ - $N_1$  subspace. The parameter values used for these panels are  $c_1 = c_2 = 2.0$ ,  $d_1 = d_2 = 0.04$ ,  $b_{11} = b_{12} = b_{21} = b_{22} = 0.05$ ,  $f_1 = f_2 = 0.3$ ,  $a_{11} = a_{22} = 0.5$ ,  $a_{21} = a_{12} = 0.25$ , and  $h_{11} = h_{12} = h_{21} = h_{22} = 0.1$ . (C) The two-dimensional view of the two consumer isoclines are shown in the subspace of the two resource axes and (D) the two-dimensional view of the two resource isoclines are shown in the subspace of the two consumer axes. (E and F) The relationships between the two resource isoclines and one of the consumer isoclines in the  $R_i$ - $N_j$  face. For a resource to invade the community where one consumer and the other resource are present at their equilibria, the invading resource's isocline must intersect the consumer's isocline above the point where the consumer's isocline intersects the other resource's isocline in this face.

consumer  $j$  when feeding on only the other resource (Holt 1977). In words, each resource's isocline must intersect a consumer's axis above where the consumer's isocline intersects the other resource's isocline when the

abundance of the resource in question is zero (e.g., Fig. 1C,D). However, with  $h_{ij} > 0$ ,  $c_i/a_{ij}$  can be less than  $N_j^*$  and  $R_i$  can still invade (Fig. 5E,F; see also Krivan and Eisner 2006). In each of Fig. 5C and D, the

equilibrium abundances for the consumer and resource identified on the axes when the other resource is absent is the point where their isoclines intersect. For the other resource to be able to invade, its isocline must pass above this point in this face. Thus, the saturating functional response on one resource increases the apparent competitive ability of the other resource because of consumer satiation by feeding on the other resource. As inequality 6 demonstrates, this has no effect on whether the equilibrium exists.

Saturating functional responses also expand the possible dynamics for the entire system. As when only one resource is present, the system displays a limit cycle or chaos if one or both resources “have a hump” and when a consumer isocline intersects an ascending portion of one of the resource isoclines (Rosenzweig and MacArthur 1963, Rosenzweig 1969). However, small areas of parameter space exist in which neither prey isocline “has a hump” (i.e., the maximum value of the resource isoclines on the consumer axes are above the point where they intersect the consumer axes) but the system displays a limit cycle or chaos (e.g., Fig. 6). Again, if one or more species display limit cycles or chaotic dynamics, more consumers than resources may coexist (Armstrong and McGehee 1976, 1980, McGehee and Armstrong 1977). Because the consumer isoclines remain planes that run parallel to all consumer axes, the maximum number of coexisting consumers still cannot exceed the number of resources for a stable point equilibrium. In addition, all the same outcomes as illustrated in Fig. 4 are possible with three or more resources. However, saturating functional responses (1) increase the equilibrium resource abundances via consumer satiation but equilibrium consumer abundances may increase or decrease, (2) allow resources with poorer apparent competitive abilities to invade and coexist, and (3) expand the possible community dynamics to include limit cycles and chaos, which may permit more consumers than available resources to coexist.

#### ADDING DIRECT CONSUMER INTRASPECIFIC DENSITY DEPENDENCE

In Eqs. 1 and 4, the density dependences that regulate the consumers’ abundances emerge as indirect effects of resource limitation. However, consumers may do many things in addition to depleting resources that will directly limit their own abundances in a negatively density-dependent fashion (Tanner 1966). Territoriality and despotic habitat filling (Pulliam and Danielson 1991, McPeck et al. 2001b, Both and Visser 2003, López-Sepulcre and Kokko 2005), cannibalism (Fox 1975, Polis 1981, Van Buskirk and Smith 1991, Rudolf 2007), opportunity costs and physiological stress due to agonistic interactions (Marra et al. 1995, Lochmiller 1996, McPeck et al. 2001a, McPeck 2004), mate finding and competition for mates (Zhang and Hanski 1998, Bauer et al. 2005, M’Gonigle et al. 2012), etc., all can generate direct intraspecific density dependence in consumers (or

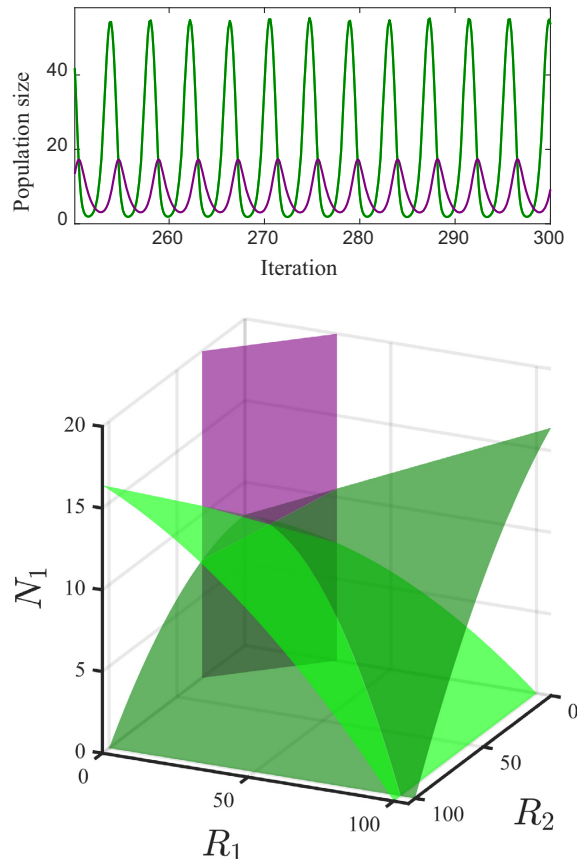


FIG. 6. An example where a stable limit cycle occurs for a two-resource and one-consumer system where the consumer has a saturating functional response, but the resource isoclines are monotonically decreasing as their own abundances increase (i.e., they have no “hump” as identified in Rosenzweig [1969]). The top panel shows the abundance dynamics for the three species, and the bottom panel shows the isoclines for the three species. In the three-dimensional panel, the origin of the axis system is at the intersection point of the three faces in the back corner. All isoclines are colored as in Fig. 1 and the parameter values used for this figure are  $c_1 = c_2 = 4.0$ ,  $d_1 = d_2 = 0.04$ ,  $b_{11} = b_{21} = 0.1$ ,  $f_1 = f_2 = 1.2$ ,  $a_{11} = a_{21} = 0.5$ , and  $h_{11} = h_{21} = 0.02$ .

resources for that matter) by reducing either their per capita birth rates or increasing their per capita death rates as their own abundances increase, and these will occur independent of their foraging abilities. Consumers may also reduce their own feeding rates because of agonistic interactions while foraging (Beddington 1975, DeAngelis et al. 1975). Thus, two ways to incorporate direct intraspecific density dependence into the consumer Equations of 1 and 4 are by either making the consumer’s per capita death rate increase or per capita birth rate decrease as its own abundance increases, or by reducing the rate at which it captures prey as its own abundance increases.

Both of these means of directly generating consumer intraspecific density dependence have been incorporated here (i.e., the consumer’s abundance now appears in the equation defining its per capita population growth rate)

in addition to the indirect effects caused by resource depletion

$$\begin{aligned} \frac{dR_i}{R_i dt} &= c_i - d_i R_i - \left( \sum_{j=1}^q \frac{a_{ij} N_j}{1 + \sum_{i=1}^2 a_{ij} h_{ij} R_i + l_j N_j} \right) \\ \frac{dN_j}{N_j dt} &= \frac{\sum_{i=1}^2 a_{ij} b_{ij} R_i}{1 + \sum_{i=1}^2 a_{ij} h_{ij} R_i + l_j N_j} - f_j - g_j N_j \end{aligned} \quad (7)$$

The  $-g_j N_j$  term in each consumer's equation can be interpreted as specifying either the increase in the consumer's per capita death rate (i.e., the intrinsic death rate term minus this term) or the decrease in the consumer's per capita birth rate (i.e., numerical response term minus this term) with its own abundance (Gilpin 1975, Gatto 1991, Caswell and Neubert 1998, Neubert et al. 2004, Chesson and Kuang 2008, McPeck 2012, 2014, Gavina et al. 2018). Additionally, the functional response is now of the Beddington-DeAngelis form where  $l_j$  scales the strength of intraspecific interference among consumer individuals while foraging (Beddington 1975, DeAngelis et al. 1975). DeAngelis et al. (1975) showed that the inclusion of both forms of intraspecific density dependence greatly increased the range of parameter space in which a stable equilibrium resulted for a one-consumer-one-resource community (see also McPeck 2012), and extensive computer simulations of Eq. 7 with two consumers and two resources show that this remains true even with saturating functional responses. I include both forms of direct intraspecific density dependence for the consumers to illustrate that they have qualitatively identical consequences for the resulting overall community structure.

#### *Direct intraspecific density dependence in consumer birth or death rate*

First consider the case with linear functional responses for the consumers (all  $h_{ij} = 0$ ) and no interference while foraging (all  $l_j = 0$ ). With  $g_j > 0$ , inequality 2 is no longer a criterion for coexistence of two consumers feeding on two resources. To see why, first consider the community depicted in Fig. 7A in which  $N_1$  is a better resource competitor than  $N_2$  on both resources (i.e.,  $f_1/(a_{11}b_{11}) < f_2/(a_{21}b_{21})$  for both  $i$ ) and neither consumer experiences any direct intraspecific density dependence ( $g_j = 0$ ).  $N_1$ 's isocline intersects both resource axes below that of  $N_2$ , and so the  $N_1$  and  $N_2$  isoclines can never intersect. Thus,  $N_1$  drives both resources to levels below which  $N_2$  cannot support a population. The result in this case is an apparent competition community module with only  $N_1$  coexisting with  $R_1$  and  $R_2$  (Fig. 7A).

In contrast, if  $N_1$  directly limits its own abundance ( $g_1 > 0$ ), the two consumer isoclines will intersect (Fig. 7B). This direct intraspecific density dependence causes its isocline to now tilt away from its own axis at a slope of  $a_{11}b_{11}/g_1$  along each  $R_i$  axis but still intersect each  $R_i$  axis at  $f_1/(a_{11}b_{11})$  (DeAngelis et al. 1975, McPeck 2012, 2017b). With only  $N_1$  present,  $N_1$  will equilibrate at a lower abundance and the two resources will equilibrate at higher abundances as compared to when  $g_1 = 0$ , and greater values of  $g_1$  cause these shifts in equilibrium abundance to be larger. If the resource abundances are increased enough,  $N_2$  can now invade and coexist with  $N_1$ . This occurs when  $g_1$  is large enough to tilt  $N_1$ 's isocline so that the intersection with the  $N_2$  isocline also crosses the intersection line of the two resources (Fig. 7B). In other words,  $N_1$  experiences enough direct intraspecific density dependence to increase the combined abundances of the two resources to levels that permit the second consumer to invade. If both consumers experience some degree of direct density dependence (i.e., both  $g_j > 0$ ), then each of their isoclines tilt away from their own axes but run parallel to the axis of the other consumer (Fig. 7C). As a result,  $N_1$ 's abundance increases,  $N_2$ 's abundance decreases, and the abundances of both resources increase, as compared to when only  $g_1 > 0$  (cf. Fig. 7B,C). However, it is important to note that the only criterion for  $N_2$  to invade is that it can increase when rare (i.e., it can satisfy its invasibility criterion); the level of direct intraspecific density dependence that  $N_2$  imposes on itself or the degree to which its abundance is shaped by the indirect effects of resource limitation as its abundance increases are both irrelevant to whether it can coexist with  $N_1$ . These factors will certainly influence its equilibrium abundance once it invades, but not whether this species is present in the community.

Including a saturating functional response (i.e.,  $h_j > 0$ ) with this form of intraspecific density dependence reduces each consumer's abundance even more. Handling time increases the point at which each consumer isocline intersects each resource axis (see above) and so moves each consumer isocline away from the origin. More importantly, a saturating functional response combined with this direct intraspecific density dependence causes the consumer isocline to become concave and asymptote at a maximum consumer abundance (Fig. 7D) (Gatto 1991, McPeck 2012, 2017b). Thus, the consumers equilibrate at even lower abundances and the resources at even higher abundances when the consumers experience both direct intraspecific density dependence and the feeding limitation imposed by handling times.

Because this form of direct consumer density dependence does not alter the resource isoclines in any way, the apparent competitive abilities of the resources promoting or preventing coexistence remain unchanged. However, resources with lower apparent competitive abilities could invade and coexist because the consumers equilibrate at even lower abundances.

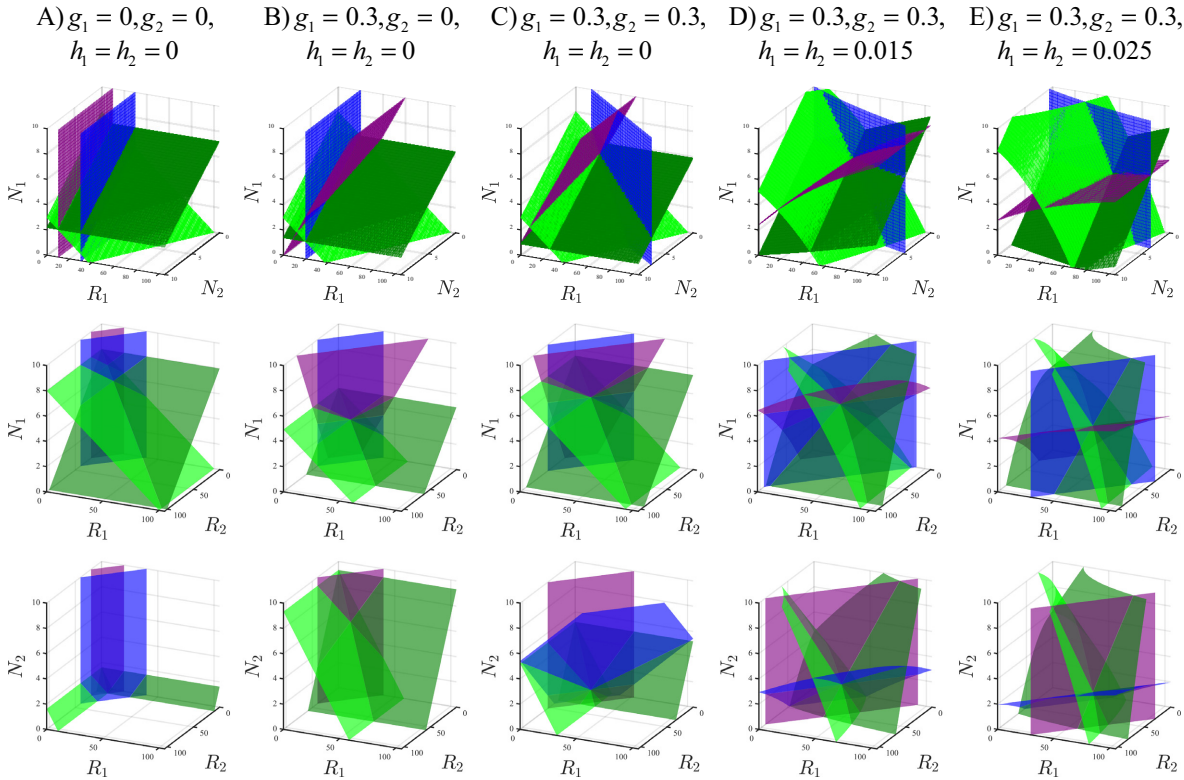


FIG. 7. Isocline portraits illustrating the differences caused by intraspecific density dependence in the consumer death rates and linear or saturating functional responses, when consumer 1 is a better resource competitor for both resources. All of these phase portraits are representations of Eq. 7 at a stable three- or four-species equilibrium, with various parameter value combinations. Each column of panels shows the phase portraits in three different subspaces for parameter combinations, with the relevant parameter values given above the column. The parameter values that are the same in all panels are  $c_1 = c_2 = 4.0$ ,  $d_1 = d_2 = 0.04$ ,  $b_{11} = b_{12} = b_{21} = b_{22} = 0.1$ ,  $l_1 = l_2 = 0.0$ ,  $f_1 = f_2 = 1.0$ ,  $a_{11} = a_{21} = 0.5$ , and  $a_{12} = a_{22} = 0.25$ . (A) When both consumers experience no intraspecific density dependence in their death rates, consumer 2 cannot coexist with consumer 1, and so only a three-species equilibrium exists. (B) If consumer 1 experiences a sufficient level of intraspecific density dependence in its death rate, the two consumers can coexist on the two resources. (C) This column of panels shows coexistence of all four species when both consumers experience some level of intraspecific density dependence in their death rates. (D and E) When combined with intraspecific density dependence in the consumer death rates, increasing the handling times of both consumers above zero causes both their isoclines to become concave and asymptote at a maximum value of their own abundance.

#### *Intraspecific density dependence in consumer foraging*

Now consider the effects of direct intraspecific density dependence in the consumer that is generated by interference while foraging (i.e.,  $l_j > 0$ ). Because this form of density dependence affects the functional response, the shapes of both the resource and consumer isoclines are altered. As with the other form of direct density dependence, feeding interference causes the consumer's isocline to tilt away from its own axis (Fig. 8). However, feeding interference also causes the resource isocline to become convex, and its intersection with the consumer isocline increases with increasing  $l_j$  (Fig. 8). With an interference level that causes  $c_i l_j > a_{ij}$ , the resource isocline develops a singularity that causes it to asymptote with increasing consumer abundance at a minimum resource abundance (DeAngelis et al. 1975). Thus, feeding interference will always increase the equilibrium abundances of the

resources because of the tilt in the consumer isoclines, but it may either increase or decrease the consumers' equilibrium abundances depending on specific parameter combinations that influence both consumer and resource isoclines.

Here too, the tilt in the consumer isoclines because of feeding interference permits a consumer that is a poorer competitor on both resources to coexist with a consumer that is a better competitor for both resources (Fig. 8). When the consumers have both nonzero handling times and feeding interference, the consumer isoclines remain planes, but they tilt away more from their own axes with higher values of handling time (i.e., their slopes become more shallow in the  $R_i-N_j$  faces). At low levels of feeding interference, the singularity in the resource isocline occurs at a negative resource abundance (i.e.,  $c_i l_j < a_{ij}$ ); in this case, the resource isoclines are concave when feeding interference is weak (i.e., as in Fig. 6) but convex when feeding

interference is stronger (Fig. 8C). However, if feeding interference is strong enough to cause the resource isocline to asymptote at a positive resource abundance (i.e.,  $c_i l_j < a_{ij}$ ), the resource isoclines are always convex in the direction of the consumer axes. In both these cases, each resource's isocline is also farther from the other resource's axis at higher abundances of the other resource (i.e., as described in the previous section and as in Fig. 6; Fig. 8C). Consequently, an increased handling time coupled with feeding interference generally increases the equilibrium abundances of both consumers and resources (cf. Fig. 8B,C).

The other major consequence of the consumers having negatively density-dependent birth or death rates or feeding interference is that the number of coexisting consumers is not limited by the number of available resources, even when the system will come to a stable point equilibrium: More consumer species than resource species can coexist. Precise conditions about the requirements for a third consumer to coexist on two resources are impossible to specify, because the possibilities for various relationships are quite large. However, as when multiple consumers coexist on a single resource (Vance 1985, McPeck 2012, 2017b), the isocline of the third consumer must intersect the  $R_1$ – $R_2$  face along a line that is closer to the origin than the point defined by the resource's equilibrium abundances with only  $N_1$  and  $N_2$  present; in other words, the invading third consumer has a positive population growth rate when rare. Here again, note that the level of direct intraspecific density dependence that this third consumer imposes on itself or the degree of self-limitation that emerges from the indirect effect of resource limitation as its abundance increases are both irrelevant to whether it can invade and coexist in the community: The only issue that is relevant is whether it can satisfy its invasibility criterion. Once this third consumer is established, the resources will equilibrate at lower abundances, and a fourth consumer may be able to invade if it can increase at this new set of resource abundances. This would continue until no other consumer is available to colonize that can invade at the equilibrium abundances of the resources, given the other consumers that are present in the community. Thus, with either form of direct intraspecific density dependence in consumers combined with resource limitation, more than two consumers can coexist on two resources at a stable point equilibrium, because these direct forms of intraspecific density dependence increase the total number of factors limiting the consumers' abundances (Levin 1970).

#### RECASTING THESE MODELS INTO LOTKA-VOLTERRA COMPETITION

Following MacArthur (1969, 1970, 1972), these models can be recast into the Lotka-Volterra competition framework by subsuming the dynamics of the resources into the consumer equations. For algebraic simplicity, I will only consider linear functional responses and no

feeding interference (i.e., all  $h_j = l_j = 0$ ) in model 7 in this section. This recasting is accomplished by assuming that resource abundances are always at equilibrium with respect to the current consumer abundances: The equation for the per capita population growth rate of each resource is set equal to zero, solved for the equilibrium resource abundance, and then substituted into the consumer equations (MacArthur 1969, 1970, 1972). By doing so, Eq. 7 for  $p$  resources and  $q$  consumers becomes

$$\begin{aligned} \frac{dN_j}{N_j dt} &= \left[ \sum_{i=1}^p a_{ij} b_{ij} \left( \frac{c_i}{d_i} \right) - f_j \right] - \left[ \sum_{i=1}^p \frac{b_{ij} a_{ij}^2}{d_i} + g_j \right] N_j \\ &\quad - \sum_{k=1 \atop j \neq k}^q \left[ \left[ \sum_{i=1}^p \frac{b_{ij} a_{ij} a_{ik}}{d_i} \right] N_k \right] \\ &= r_j - \alpha_{jj} N_j - \sum_{k=1 \atop j \neq k}^q \alpha_{jk} N_k \end{aligned} \quad (8)$$

(cf. Eq. 3 of MacArthur 1969 or Eq. 3 of Chesson 1990). MacArthur's formulation of Lotka-Volterra competition differs from the typical formulation in one very important respect. The typical formulation (e.g., Volterra 1926, Lotka 1932, Gause 1934, Slobodkin 1961, Strobeck 1973) is a modification of exponential population growth in which the intrinsic rate of increase is multiplied by a reduction factor that is a function of species abundances

$$\frac{dN_j}{N_j dt} = r_j \left( 1 - \frac{\sum_{k=1}^q \alpha_{jk} N_k}{K_j} \right).$$

In this more typical formulation, the intrinsic rate of increase plays no role in species coexistence, but rather the ratios of the carrying capacities have a similar effect (Strobeck 1973, Vandermeer 1975). In contrast, in MacArthur's (1969, 1970, 1972) formulation, differences among competitors in their intrinsic rates of increase, and not carrying capacities, are essential to whether they can or cannot coexist. Vandermeer (1975) provides an excellent comparison of the two formulations. The first square bracketed term in Eq. 8 is the intrinsic rate of increase for the consumer ( $r_j$ ). Note that this term is exactly the population growth rate of the consumer when it invades a community consisting of all the resources at their equilibrium abundances in the absence of all consumers (i.e.,  $R_i^* = c_i/d_i$ ). The second bracketed term in Eq. 8 is the intraspecific competition coefficient defining the per capita decrease in per capita population growth rate ( $\alpha_{jj}$ ), which contains both the intraspecific indirect density-dependent effect due to resource limitation (first term inside the bracket) and the direct

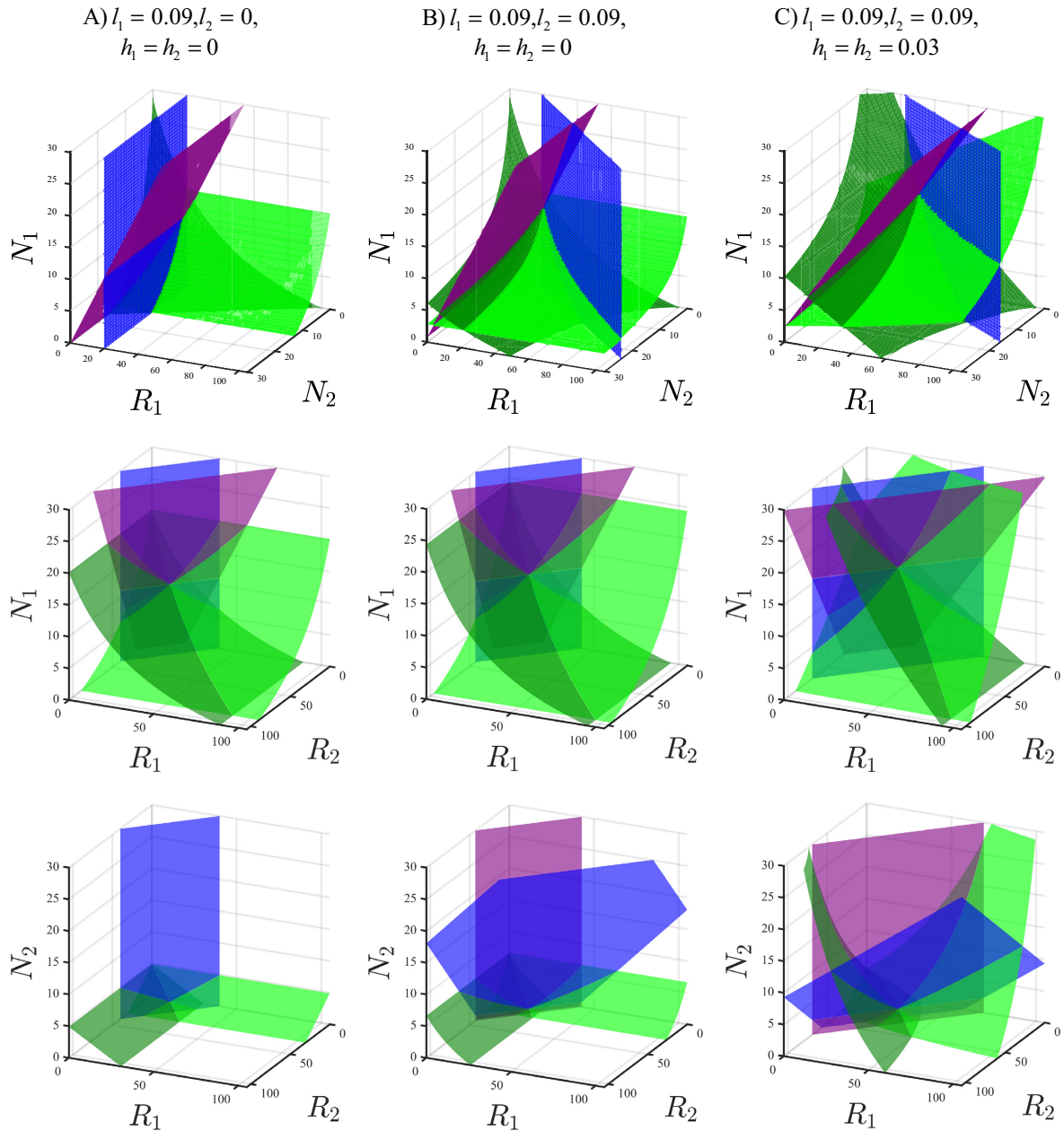


FIG. 8. Isocline phase portraits illustrating the differences caused by intraspecific feeding interference among the consumers and linear or saturating functional responses, when consumer 1 is a better resource competitor for both resources. All of these phase portraits are representations of Eq. 7 at a stable four-species equilibrium, with various parameter value combinations. Each column of panels shows the phase portraits in three different subspaces for parameter combinations, with the relevant parameter values given above the column. The parameter values that are the same in all panels are  $c_1 = c_2 = 4.0$ ,  $d_1 = d_2 = 0.04$ ,  $b_{11} = b_{12} = b_{21} = b_{22} = 0.1$ ,  $f_1 = f_2 = 1.0$ ,  $g_1 = g_2 = 0.0$ ,  $a_{11} = a_{21} = 0.5$ , and  $a_{12} = a_{22} = 0.25$ . The column of panels in Fig. 6A shows phase portraits when neither consumer experiences intraspecific feeding interference for comparison, and so only consumer 1 will coexist with the two resources. The four species can coexist at a stable equilibrium (A) if only consumer 1 or (B) both consumers experiences a sufficient level of intraspecific feeding interference. (C) Increasing the handling time of the consumers increases the equilibrium abundances of the resources, as it does with intraspecific density dependence in the consumer death rates. However, unlike intraspecific density dependence in consumer death rates, increasing handling times with intraspecific feeding interferences causes the equilibrium consumer abundances to increase.

intraspecific density dependence effect (second term). The inner square brackets in the end summation are the interspecific competition coefficients ( $\alpha_{jk}$ ).

The components of these competition coefficients due to resource limitation are then understood as reducing the maximum possible growth rate of the

consumer, its intrinsic rate of increase as defined here, by the feeding losses it incurs via resource removal by each consumer species, including itself. To see this, rewrite Eq. 8 by collecting terms due to resource limitation and due to other factors separately

$$\begin{aligned} \frac{dN_j}{N_j dt} &= \left[ \sum_{i=1}^p a_{ij} b_{ij} \left( \frac{c_i}{d_i} - \frac{a_{ij}}{d_i} N_j - \sum_{\substack{k=1 \\ j \neq k}}^q \frac{a_{ik}}{d_i} N_k \right) \right] \\ &\quad - f - g_j N_j \\ &= \sum_{i=1}^p a_{ij} b_{ij} R_i^* - f - g_j N_j \end{aligned} \quad (9)$$

(compare these equations to the corresponding ones in Eq. 7 with  $h_j = l_j = 0$ ). The square brackets in these equations contain all the components of resource limitation that contribute to the regulation of each consumer population. The inner parentheses inside this square bracket expresses  $R_i^*$  as its abundance in the absence of all consumers (i.e.,  $c_i/d_i$ ) minus the decrements due to feeding by each consumer (remember that this approach is predicated on the resources being at equilibrium with respect to the current consumer abundances, hence the designation of this as an equilibrium abundance of  $R_i^*$ ). The amount of resource  $i$  decremented because of feeding by the consumer in question is  $a_{ij} N_j / d_i$ ; this is the measure of the (intraspecific) indirect effect of the consumer on itself generated by resource limitation. Likewise, each consumer  $k$  has reduced resource  $i$ 's abundance by  $a_{ik} N_k / d_i$ , which is the measure of the interspecific indirect effect of resource limitation for consumer  $k$ . Resource abundances directly influence each consumer's population dynamics, but the Lotka-Volterra framework expresses resource abundances in terms of how much has been removed by each consumer. This is why resource limitation appears as direct interactions with the other consumers in this formulation.

Given this model, two consumers must satisfy the classic inequality

$$\frac{\alpha_{11}}{\alpha_{21}} > \frac{r_1}{r_2} > \frac{\alpha_{12}}{\alpha_{22}} \quad (10)$$

to coexist at a stable equilibrium, with terms as defined in Eq. 8 (this is identical to inequality 6.25 of May 1973, inequality 4 of Vandermeer 1975, and inequality 13 of Chesson 1990). The “rule of thumb” that coexistence requires each species to limit its own abundance more than it limits the abundances of other species (e.g., Chesson 2000, Adler et al. 2007, Levine and HilleRisLambers 2009, Godoy and Levine 2014) (i.e.,  $\alpha_{11} > \alpha_{21}$  and  $\alpha_{22} > \alpha_{12}$ ) is consistent with the interpretation of this inequality, but strictly only if the two species have identical intrinsic rates of increase.

Fig. 9 presents the recast Lotka-Volterra competition parameters (Eq. 8) for the underlying parameter

combinations given in all panels in Fig. 4 and in panels A–C of Fig. 7. In all these various parameter combinations, inequality 10 is satisfied for each pair of species that coexist and is not satisfied for pairs of species that do not coexist. However, if one only applied the “rule of thumb” that each species must limit its own abundance more than it limits the abundances of other species (i.e.,  $\alpha_{jj} > \alpha_{kj}$ ), a number of these scenarios would appear to contradict what is needed for coexistence. Specifically, the Lotka-Volterra competition coefficients resulting from the scenarios in Figs. 4C and 7B,C do not match this rule of thumb. For Fig. 4C, the one consumer,  $N_3$ , that coexists with the three resources does have its intraspecific competition coefficient greater than both interspecific coefficients, and one of the excluded consumers,  $N_2$ , has an intraspecific coefficient that is smaller than one of its interspecific coefficients (Fig. 9C). However,  $N_1$  has its intraspecific coefficient greater than both interspecific coefficients, and yet this species is excluded from the community (Fig. 9C). In contrast, the two consumers coexist in Fig. 7B,C, but  $N_2$  has an intraspecific competition coefficient that is smaller than its interspecific competition coefficients in both scenarios (Fig. 9F–G). These three scenarios clearly illustrate that the relative strengths of the Lotka-Volterra coefficients cannot simply be compared in isolation: The ratios of competition coefficients relative to the ratio of the intrinsic growth rates must be compared to evaluate coexistence in the Lotka-Volterra competition framework (May 1973, Chesson 1990, 2000, Barabás et al. 2018).

## DISCUSSION

When cast into the framework of Lotka-Volterra competition, the structure of a guild of resource competitors seems straightforward (MacArthur 1972, May 1973, Abrams 1975, Chesson 1991, 2000, Adler et al. 2007, Kleinhesselink and Adler 2015). For coexistence, each species is supposed to limit its own abundance more than it limits the abundances of other species. This presumption implies that demographic trade-offs cause species to have distinct advantages that favor their population growth rates when they are rare but have distinct disadvantages that restrict their population growth rates when they are abundant (Chesson 1991, 2000, Adler et al. 2007). However, even in the simple models that MacArthur propounded, this simple rule of thumb is not dispositive. The relative strengths of intraspecific and interspecific limitation must be evaluated relative to the ratio of intrinsic rates of increase of competing species (MacArthur 1972, May 1973, Chesson 1990, 2000, Barabás et al. 2018).

This simplified view of community structure also masks the essential mechanisms that foster or retard invasibility by shifting focus away from the proximate features that promote coexistence in multispecies assemblages across trophic levels. In the Lotka-Volterra competition framework, the consumer's growth rate when

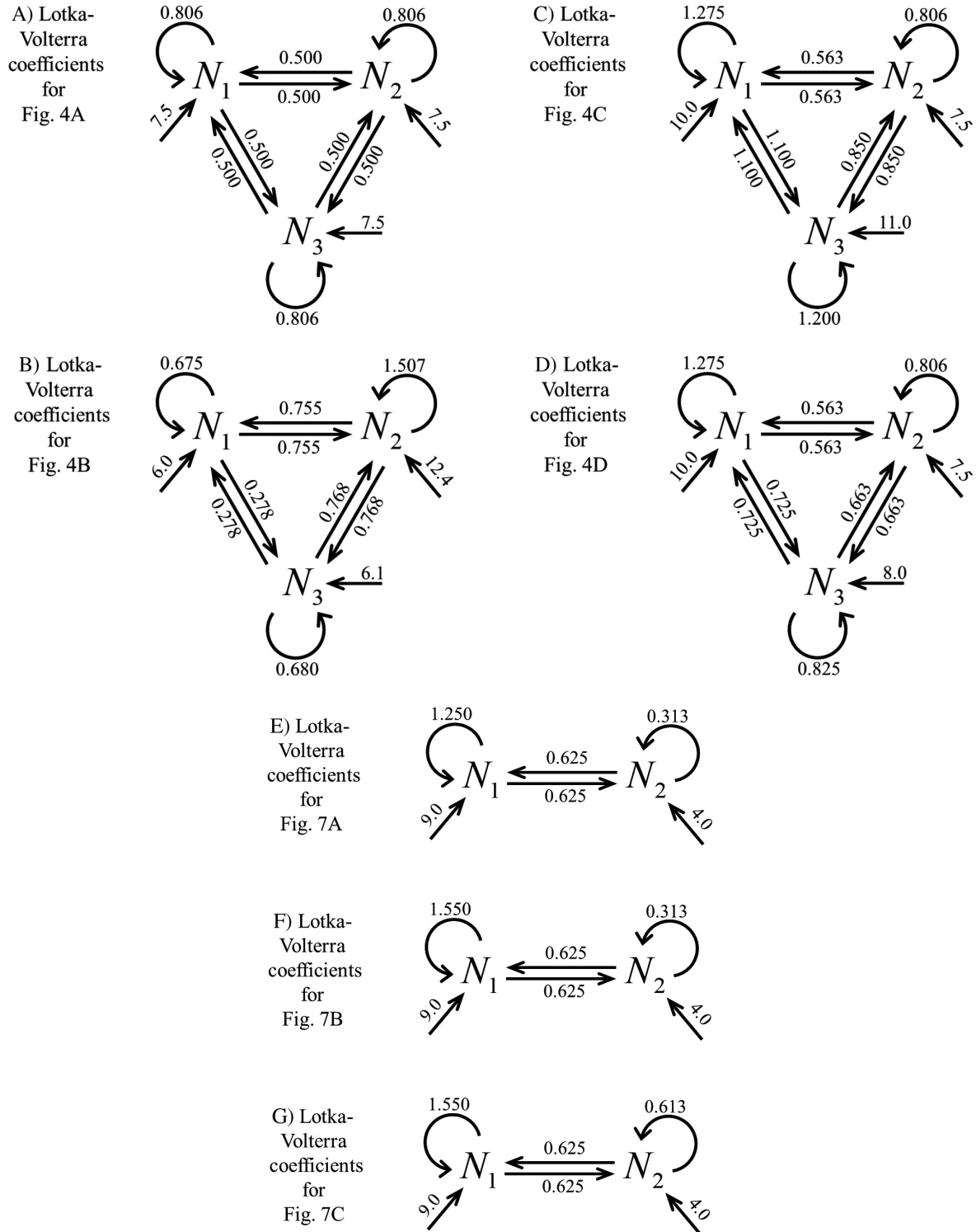


FIG. 9. Parameters estimated for the recast Lotka-Volterra competition form of Eq. 7 for the underlying parameter combinations illustrated in (A) Fig. 4A, (B) Fig. 4B, (C) Fig. 4C, (D) Fig. 4D, (E) Fig. 7A, (F) Fig. 7B, and (G) Fig. 7C. The underlying parameters for each panel are given in the corresponding previous figure. Numbers associated with arrows in each panel are the Lotka-Volterra competition parameter estimates derived from Eq. 8: Numbers associated with circular arrows from and to consumer  $j$  are intraspecific competition coefficients ( $\alpha_{jj}$ ), with arrows from consumer  $k$  to consumer  $j$  are interspecific competition coefficients ( $\alpha_{jk}$ ), and with arrows pointing at the consumer  $j$  identifier are the intrinsic rates of increase ( $r_j$ ).

all resources are at their equilibrium abundances in the absence of all consumers (i.e., the intrinsic rate of increase) is an essential component to evaluate coexistence (i.e., inequality 10), but the critical growth rate for evaluating coexistence is the consumer's growth rate when invading a community that already contains all the other consumers at equilibrium with the resources (MacArthur 1972, Holt 1977, Chesson 2000, Siepielski and McPeck 2010). Likewise, the focus on the relative strengths of intraspecific and interspecific competitive abilities quantified in the Lotka-Volterra framework is similarly misplaced. To see this, consider the parameter combinations considered in Figs. 7A–C and 9E–G. The consumer that is the superior competitor on both resources (i.e.,  $N_1$ ) will be present in the community regardless of whether the consumer that is the subordinate competitor on both resources (i.e.,  $N_2$ ) is present (i.e., the superior consumer can always invade). Whether the inferior resource competitor can coexist with the superior resource competitor depends solely on whether it has a positive population growth rate at the resource abundances that result when only the superior competitor is at equilibrium with the resources (i.e., when  $N_2$  invades the community with  $N_1$  already present and at equilibrium). The inferior competitor's intrinsic rate of increase, its ability to affect the growth rate of the superior competitor by depleting the resources, and the magnitude of both indirect and direct density-dependent effects it has on itself are all irrelevant to whether it will coexist with the superior competitor. When these two consumers can coexist, inequality 10 is satisfied as an emergent property, but the reasoning that is derived from the interpretation of this inequality (i.e., the ratio of intrinsic rates of increase relative to the strengths of intraspecific vs. interspecific competition) does not explain why each can coexist with the other. The same is true if feeding interference limits the superior consumer (Fig. 8).

Even in the simplest consumer–resource model considered here where only resource species directly limit their own abundances and consumers have linear functional responses (i.e., Eq. 1), these types of generalities do not truly explain why consumers or resources coexist when more than two resources are available. A specific set of trade-offs in both the resource competitive abilities of consumers and the apparent competitive abilities of resources are required for two consumers and two resources to coexist (Fig. 1). With more than two species at each trophic level even in this simplest model, many different configurations of resource and apparent competitive abilities among the consumers and resources will result in multiple species at both trophic levels coexisting, and many outcomes do not conform to the intuition derived from Lotka-Volterra competition that each species must have some demographic advantage when rare (see also Levene 1976, Abrams 1988, 1998). For example, an inferior competitor on each of the available resources (i.e., a species that has  $f_i/(a_{ij}b_{ij})$  values that are

not the lowest for any single available resource) may drive an entire collection of individually superior consumers (i.e., species that have the lowest  $f_i/(a_{ij}b_{ij})$  value on at least one available resource) extinct, or an inferior competitor on each of the available resources may be able to coexist with a different set of individually superior competitors (Fig. 4). Additionally, differences in productivity among resources can cause the exclusion of a superior competitor because other resources inflate the abundance of an inferior competitor feeding on its preferred resource, which also distorts the interpretations one can make via the recasting to Lotka-Volterra competition (Abrams 1998). In all these cases, inequality 10 is satisfied, but again the mechanistic reasons why these consumers and resources coexist are not embedded in the interpretation of this inequality; this mechanistic understanding is found in how the abilities of these various consumers to feed on the resources and the relative productivities of the resources determine the strengths of the direct and indirect interactions of resource and apparent competition (Tilman 1987).

Saturating functional responses of consumers do not fundamentally alter the qualitative structure of communities at stable point equilibria, but they do increase the scope of dynamics for the system and the range of resources that can exist in the community. As in models with fewer species, limit cycles and chaotic population dynamics around equilibria occur in some areas of parameter space (Rosenzweig and MacArthur 1963, Krivan and Eisner 2006), and this is true even in some areas where resource isoclines are monotonically descending over the entire range of resource abundances. Previous analyses have demonstrated that consumer cycling dynamics can permit more consumer species than resource species to coexist (Armstrong and McGehee 1976, 1980, McGehee and Armstrong 1977). The other important change caused by saturating functional responses is to increase the range of apparent competitive abilities for resources that can invade a particular community (Fig. 5E,F; see also Krivan and Eisner 2006).

However, a much broader range of possibilities emerges when resource-limited consumers also directly limit their own abundances in a negative density-dependent fashion. Even when only two resources are available, more than two consumers can coexist at a stable point equilibrium if the best resource competitor experiences an adequate level of intraspecific density dependence, either via interference while feeding or from other demographic processes (Figs. 7, 8). This is not surprising, given that previous analyses have shown that multiple consumers can coexist on a single resource species (e.g., Vance 1985, McPeck 2012). Interestingly, MacArthur (1970) very briefly pondered the effect of a direct density-dependent consumer death rate (i.e., the  $-g_i N_i$  term in Eq. 7), but concluded that it did not affect the basic outcome. The importance of such direct intraspecific density dependence is not apparent until one realizes that such effects reduce the ability of the

consumer to deplete the resources, and so make resources available to poorer competitors that would be excluded otherwise (i.e., Figs. 7, 8): an issue that is not apparent when viewed from the perspective of Lotka–Volterra competition. Adding other types of species to the community that would also limit the abundances of consumers (e.g., specialized predators, parasitoids, or disease-causing organisms), and so increase the levels of available resources for poorer competitors, would have the same effects as direct intraspecific density dependence modeled here (Grover 1994).

The operation of these processes also greatly expands the possible constellation of species properties that would foster coexistence among consumers. The typical expectation for feeding abilities among resource competitors implies that coexisting consumers would rank resources in different orders in their diets (e.g.,  $a_{11} > a_{21}$  but  $a_{12} > a_{22}$  is a very easy parameter combination to satisfy inequalities (2) and (3), assuming all consumers have similar conversion efficiencies). However, if both resource availabilities and consumer abundances directly limit consumer per capita growth rates in a density-dependent fashion (e.g., Figs. 7–8), consumers can easily display nested hierarchical resource preferences (e.g., Pires et al. 2011), as are already well documented for mutualisms (Bascompte et al. 2003, 2006, Jordano et al. 2003, Dáttilo et al. 2014). As in other types of community modules (McPeck 2012, 2014, 2017b), various forms of direct intraspecific density dependence greatly increase the scope of coexistence among consumers, and specifically facilitate community membership for a greater number of substantially poorer competitor species.

### *Conceptual views of community structure*

Given the substantially greater range of potential outcomes that are masked and the obfuscation of mechanisms that occur in the Lotka–Volterra competition approach, we should heed Tilman’s (1982) advice that it is much more informative to base our understandings and predictions about how resource competition may structure a guild of consumers on the models that directly explore these mechanisms. Tilman (1980, 1982) developed his graphical approach to various resource types using ZNGI’s (i.e., consumer isoclines in resource abundance space) and consumption vectors to explore how the direct and indirect interactions among these species shape community structure. Leibold (1998) showed how Tilman’s approach applies to apparent competition and diamond/keystone community modules (see also Chase and Leibold 2003). Kleinhesselink and Adler (2015) and Letten et al. (2017) have also recently explored the explicit linkages between the ZNGI/consumption vector approach and Lotka–Volterra competition.

Two important assumptions must be made for the ZNGI/consumption vector approach to be valid: the consumer and resource isoclines must each be

independent of their own abundances, and only two resources are available. The first assumption is what permits the graphical approach to map inequality 3, which is a statement about how the resource isoclines intersect (Fig. 1B), onto the consumer isoclines at equilibrium in Fig. 1A. This approach can be extended to many other resource types besides perfectly substitutable (e.g., Tilman 1980, 1982, Fox and Vasseur 2008, Kleinhesselink and Adler 2015). The analyses presented here also suggest that the ZNGI/consumption vector approach applies equally well if the consumers have saturating functional responses (i.e., Fig. 5A and inequality 6).

The great utility of the ZNGI/consumption vector approach is that it reduces a four-dimensional dynamical problem of two resources and two consumers to a two-dimensional problem in which only the resource abundances are followed explicitly. This is possible in models 1 and 4 because the consumer isoclines are identical across the  $R_1$ – $R_2$  subspace, regardless of the combination of consumer abundances (i.e., each consumer isocline is parallel to all consumer axes), and because no consumer abundance directly influences the per capita growth rate of any consumer, including itself: Consumers only influence their own and other consumers’ abundances indirectly through their effects on determining resource abundances. However, if the abundance of either consumer is shaped by any process that makes its isocline not parallel to all consumer axes (e.g., intraspecific or interspecific interference, Allee effects), this approach will not work because not only will the resource abundances and the lengths of the consumption vectors change, but the consumer isoclines will also change in the  $R_1$ – $R_2$  subspace as consumer abundances change.

The general conclusion for coexistence from the ZNGI/consumption vector analyses is that “each species consumes proportionately more of the resource that more limits its own growth” (Tilman 1982:75). In the Lotka–Volterra competition framework, this result is translated to mean that each consumer limits its own abundance more than it limits the abundances of other species (Chesson 1990, 2000, Adler et al. 2007, Levine and HilleRisLambers 2009, Kleinhesselink and Adler 2015, Letten et al. 2017). However, these insights from the ZNGI/consumption vector approach are only valid if the consumers (or any other species besides the resource for that matter) only indirectly limit their own abundances through their effects on the resource abundances. Moreover, whether these indirect interactions with itself and with other species result in coexistence depend as much on the apparent competitive abilities of the resources as they do on the resource competitive abilities of the consumers. For example, in Tilman’s framework, the consumers will not coexist if the supply point is outside the wedge defined by the consumption vectors, but this should more generally be understood as a result of apparent competition among the resources inflating the abundance of one consumer to a level that

excludes the other consumer because of the effect that consumer has on the abundance of the preferred resource of the excluded consumer: Mechanistic understanding emerges from understanding the tangled web of apparent and resource competitive indirect effects.

The results presented here also show that this general requirement for coexistence of two consumers feeding on two resources does not extend to communities where three or more resource species are available (e.g., Fig. 4). I know of no analysis that has extended the ZNGI/consumption vector approach to more than two resources. With three or more resources, constructing scenarios where one or more consumers that are subordinate competitors on all resources coexist in a community that is saturated with consumers is rather easy (e.g., Fig. 4D). Thus, with more than two resources, each consumer species does not need to consume proportionately more of any single resource. Moreover, many configurations in which each consumer is best at capturing and consuming a different resource do not result in coexistence (as in the two-resource/two-consumer case), and a consumer that is a subordinate competitor on all available resources may drive all other consumers extinct (Fig. 4C). All this implies that the degree of resource overlap is not the single, critical issue determining whether relative competitive abilities will define coexistence for species that share resources (Abrams 1998, Chesson and Kuang 2008, Kleinhesselink and Adler 2015).

If other processes in addition to resource availabilities also directly limit consumer abundances, the number of resources no longer limits the number of coexisting consumers at point equilibria. Tilman accomplished this by hypothesizing fine-scale heterogeneity in the resource supply points for a local assemblage of consumers (e.g., Fig. 36 in Tilman 1982). However, no such heterogeneity is needed for consumers that are territorial (Pulliam and Danielson 1991, McPeck et al. 2001b, Both and Visser 2003, López-Sepulcre and Kokko 2005), aggressive or cannibalistic toward one another (Beddington 1975, DeAngelis et al. 1975, Smith and Van Buskirk 1991, Rudolf 2007), express stress responses to the presence of conspecifics (McPeck et al. 2001a, Glennemeier and Denver 2002), must compete for mates (Zhang and Hanski 1998, M'Gonigle et al. 2012), have diseases (Holt and Pickering 1985, Rudolf and Antonovics 2005, Bagchi et al. 2014), or have predators (Janzen 1970, Connell 1971, Grover 1994, Terborgh 2012) that also influence their demographics. In all these systems with greater complexity, the constraint on the number of coexisting species becomes the number of limiting factors (Levin 1970), including interactions with conspecifics, and not simply the number of limiting resources.

All this is not to say that very appealing conceptual insights have not emerged from the exploration of Lotka-Volterra models of competition. For example, Chesson's (2000) characterization of "equalizing" and "stabilizing" effects of species interactions identifies a critical tension

between species similarities differences that are required for coexistence: inequality 10 is the basis for separating these effects (Chesson 1990). However, these ideas should be greatly expanded to encompass mechanistic aspects of species interactions in various community modules, and so to be applied well beyond the simple construct of Lotka-Volterra competition. In fact, Leibold's (1998) expansion of the ZNGI/consumption vector framework sets the foundation for such a mechanistic expansion. He explored the similarities and differences needed among consumers drawn from a regional pool in their ZNGIs/consumption vectors for local coexistence in resource competition, apparent competition, and keystone/diamond community modules. However, as the above discussion suggests, I think a broader range of insights can be had from simply considering the full set of isoclines for a species assemblage.

Following Leibold (1998), equalizing effects are properties of species that cause their isoclines to occupy similar areas of state space so that they may intersect. A species' isocline maps the environmental conditions in which its average fitness is at replacement (Charlesworth 1994, Lande 2007, McPeck 2017a, b), and so species having similar average fitnesses implies that their isoclines may intersect. This is a much more expansive view that simply stating that their intrinsic rates of increase or average fitnesses are similar. Here again, the issue is not whether these statements about fitness are true, but rather why they are true. Imagine in Fig. 1A that  $N_2$ 's isocline fell completely above that for  $N_1$ . In this case, the two consumers would have disparate average fitnesses so that  $N_1$  would locally extirpate  $N_2$  (as in Fig. 7A). The only way they can coexist is for their average fitnesses to be more similar in this environmental setting, which implies that their isoclines intersect (Fig. 1A). The mechanistic understanding of these equalizing effects in this case (i.e., the "why") comes from knowing that these two consumers have similar resource competitive abilities (i.e., similar values of  $f_j/(a_{ij}b_{ij})$ ), and that the resource species have similar apparent competitive abilities (i.e., similar values of  $c_i/a_{ij}$ ). Comparable insights are required to understand the equalizing effects in other types of community modules (e.g., food chains, keystone/diamond modules, intraguild predation) where additional mechanisms are involved in regulating the various species abundances.

Likewise, stabilizing effects are those properties of species that cause the isoclines of all the species in the community to intersect in ways that promote their coexistence. For Leibold (1998), this was the relationships among the consumption vectors of the consumers relative to resource and predator ZNGIs, which are in fact simply statements about the relative positions of isoclines analogous to the inequalities to define stable coexistence given here (e.g., inequalities 2 and 3), or 5 and 6; see also Letten et al. 2017 who also made this point about the ZNGI/consumer consumption vector forms of these models). More generally, one can think of

stabilizing effects as the properties of species that define the shapes of their isoclines and the ways the isoclines of various species intersect to promote coexistence. Again in Fig. 1A, the mechanistic understanding of the stabilizing effect that permits the two consumers to coexist is that each is a better resource competitor on a different resource (i.e., inequality 2 is satisfied [as in Leibold 1998]). In more complicated situations, mechanistic understanding of stabilizing effects would require, for example, explaining how a consumer that is an inferior competitor on all available resources may still coexist with superior competitors by showing how it can garner adequate nutrition from many available resources while the better competitors are really successful on a smaller subset of the available resources (e.g., Fig. 4D).

Such an expansion in our conceptual inquiries about species coexistence should also guide experimental field studies of coexistence in real communities. A number of recent studies of “niche differences” among species have designed inquiries around Lotka-Volterra predictions of comparing the fitnesses/population growth rates within and among species when they are rare and abundant in communities (e.g., Inouye 2001, Sears and Chesson 2007, Levine and HilleRisLambers 2009, Adler et al. 2010, Violle et al. 2011, Godoy and Levine 2014, Godoy et al. 2014, Kraft et al. 2015). These types of studies can test the necessary conditions that a species may satisfy the invasibility criterion for a particular community (does the species have a positive population growth rate when rare and other species are at their demographic equilibrium in its absence?), and that interactions with other species in the community either directly or indirectly limit each species’ growth rate in a density-dependent fashion (Chesson 2000, Inouye 2001, Siepielski and McPeck 2010). They also can provide estimates of the Lotka-Volterra competition coefficients among species (Inouye 2001, Sears and Chesson 2007, Godoy et al. 2014).

However, interpretations of the results of these types of experiments must also recognize the assumptions that underlie these interpretations. For example, Levine and HilleRisLambers (2009) grew 10 serpentine-soil annual plants in mixed species communities and estimated per capita population growth rates for each under various conditions. They found that four species showed significant experimental responses of decreasing per capita growth rates with increasing relative abundance (i.e., interpreted as signifying “niche differences” in the Lotka-Volterra competition interpretation), three showed no significant change, and three had increasing per capita growth rates with increasing relative abundances. Likewise, Kraft et al. (2015) conducted a field experiment in which 18 annual plant species were competed against one another in pairwise combinations and found that only 12 of 102 pairwise species comparisons conformed to the Lotka-Volterra competition expectation for coexistence. Perhaps some substantial fraction of species in local assemblages are not coexisting, but rather are neutral, sink, or walking-dead species

(McPeck 2017b). However, these interpretations are all based on unstated assumptions about resource dynamics (e.g., resources are always in equilibrium with current consumer abundances), the demographic properties of these species in the experimental environment (e.g., all have very similar intrinsic rates of increase in those experimental units), and the strengths of interactions with other species not directly included in the experimental designs (e.g., pollinators, fungal mutualists, herbivores, diseases are not important influences on outcomes). For example, very different estimates of intraspecific and interspecific competition coefficients would likely be obtained if initial nutrient concentrations in the soils of experimental units were at levels representative of the long-term absence of plants vs. levels representative of the presence of the natural community of plants at equilibrium (Abrams 1998). Moreover, even if all the assumptions of the experimental design are met, these types of experiments can only evaluate whether species are coexisting, and not why they are coexisting.

The understanding of both whether and why resource competitors are coexisting would come from an integrated experimental program that directly explores the mechanisms defining their interactions in the community (Tilman 1987). Such a program would identify the set of limiting resources or prey species that shapes the indirect density-dependent interactions within and among the consumers. It would quantify the abilities of the consumers to capture those resources and drive their own population dynamics, and it would quantify the potential productivities of the various resources: together this information would define the resource competitive abilities of the consumers and the apparent competitive abilities of the resources. Such a research program would obviously quantify the strengths of intraspecific and interspecific interactions among the species as in the above studies of plants, but it would also explore the importance of processes such as feeding interference, stress responses, allelochemicals, etc., that can generate direct density dependence in the consumers that would also limit the depths to which the consumers can reduce resource abundances. Finally, such a research program would not ignore that other species in the community influence the demography of both the consumers and resources (e.g., mycorrhizal symbionts, pollinators, pathogens, higher trophic level herbivores, and predators), all of which may directly and indirectly influence the consumers and resources. No species in a community has a single process or a single interaction type that defines its entire demography, and so understanding community membership and the mechanisms that promote coexistence requires us to embrace this admittedly more complex and difficult, but ultimately more rewarding, set of approaches.

Expanding our worldview beyond Lotka-Volterra competition also makes interpretation of other types of experimental results more rational. For example, why would adding nutrients to a community not alleviate

competition and cause all species to thrive? In contrast to this expectation, the typical result of adding available nutrients to the bottom of a food web is that many algae and plant species go extinct (e.g., Goldberg and Miller 1990, Foster and Gross 1998, Leibold 1999, Grover and Chrzanowski 2004, Harpole and Tilman 2007). As most of these studies demonstrate, increasing nutrient levels typically favors one or a few plant species above all others, and other species are driven extinct because of shading by the dominant(s). When considered in the joint framework of apparent and resource competition, this result is perfectly understandable: increasing the availability of one resource inflates the abundance of one consumer (the resulting dominant plant or alga in this case) that, in turn, decreases the availability of other resources below levels at which other consumers can persist. In other words, consumers are being driven extinct because of apparent competition among the resources.

Understanding the indirect effects that cascade through a community are essential to predicting community changes, and these indirect effects should not be shrouded behind the curtain of Lotka-Volterra competition. We have known this, even for the simplest of communities, for a very long time (e.g., Levene 1976). There is no substitute for working with models that better encapsulate the mechanisms of interactions among multiple species and using these more explicit models to guide empirical investigations of coexistence. Valid empirical inquiries must not only test for general patterns consistent with coexistence (e.g., population growth rates are higher at low abundances) but also validate the operation of those mechanisms in the field (e.g., identifying which resources/prey are limiting to various consumers/predators, testing for direct intraspecific density dependence outside of resource limitation), identify the phenotypic properties of species that influence their fitnesses in these interactions, and test broader predictions that result from incorporating these mechanisms into models of community structure.

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