

# Keystone and Intraguild Predation, Intraspecific Density Dependence, and a Guild of Coexisting Consumers

Mark A. McPeck\*

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

Submitted February 14, 2013; Accepted July 8, 2013; Electronically published November 21, 2013

Online enhancement: appendix.

**ABSTRACT:** Previous models of diamond-shaped and intraguild predation community modules have represented the essence of the trade-off necessary for a top predator to prevent competitive exclusion among a set of resource-limited consumers. However, at most two consumers can coexist in these models. In this article, I show how intraspecific density dependence in the consumers can permit many more than two consumers to coexist in these community modules. Moreover, responses of the community to removal of the top predator depend on the patterns of the strengths of species interactions relative to the strengths of intraspecific density dependence. If the consumers experience similar strengths of intraspecific density dependence, removing the top predator will in most cases have little effect on consumer species richness. A substantial reduction in consumer species richness with predator removal (i.e., the keystone predation effect) will typically occur only when the consumer that can support a population at the lowest resource abundance also (1) experiences substantially weaker intraspecific density dependence than other consumers and (2) experiences significantly higher levels of mortality from the predator. These results identify how intraspecific density dependence fosters the coexistence of multiple consumers in two important community modules and shapes the responses of these community modules to perturbations such as predator removal.

**Keywords:** coexistence, community module, diamond-shaped community module, food chain module, intraguild predation, intraspecific density dependence, keystone predation, species richness.

## Introduction

One of the great conundrums of community ecology has been that many biological communities are fantastically diverse, but mechanistic models of community and food web structure struggle to predict coexistence of more than a handful of species (e.g., Hutchinson 1961; Grubb 1977; Tilman 1982). These models explore how various network configurations of interacting species (i.e., community modules) influence the number and types of species that can

invade and subsequently coexist (Holt 1997; McCann 2012). For example, coexistence of multiple resource competitors in model systems requires that each consumer be limited by a different resource (MacArthur and Levins 1964; Levin 1970; Tilman 1982), but many real communities seem to contain many more consumers than limiting resources (e.g., Hutchinson 1961; Grubb 1977; Armstrong and McGehee 1980; Tilman 1982; Chesson 1991). Adding a top predator that feeds on these competing consumers is predicted to increase the number of coexisting consumers eating each resource from one to only two: one consumer should be more limited by the basal resource and the other more limited by the predator (e.g., Levin 1970; Vance 1978; Holt et al. 1994; Leibold 1996; McPeck 1996), whereas real systems typically have high prey diversity (e.g., Paine 1966, 1974; Harper 1969; Paine and Vadas 1969; Estes et al. 1978; Duggins 1980; Menge 1995; McPeck 1998).

The problem becomes even more pernicious when we recognize that communities and food webs do not typically exist in discrete trophic levels (Polis and Strong 1996). Namely, omnivory and intraguild predation, where a predator also feeds on the resource of its prey, impose even greater constraints on species coexistence (Holt and Polis 1997; Diehl and Feiel 2000; Mylius et al. 2001; Revilla 2002; Křivan and Diehl 2005; Rudolf 2007; Amarasekare 2008). To coexist, the consumer must be a better resource competitor than its predator (Holt and Polis 1997), and high levels of resource productivity tend to prevent the intraguild predator and its prey from coexisting regardless of their relative competitive abilities (Diehl and Feiel 2000; Mylius et al. 2001; Křivan and Diehl 2005; but see Amarasekare 2008). However, real food webs typically have multiple intraguild prey coexisting with an intraguild predator (Polis et al. 1989; Winemiller 1990; Diehl 1995; Polis and Strong 1996; Woodward and Hildrew 2002; Arim and Marquet 2004).

In contrast to mechanistic models of species interactions, more phenomenological models provide a different

\* E-mail: mark.mcpeck@dartmouth.edu.

Am. Nat. 2014. Vol. 183, pp. E1–E16. © 2013 by The University of Chicago. 0003-0147/2014/18301-54484\$15.00. All rights reserved.

DOI: 10.1086/674010

perspective on coexistence. In these approaches, explicit mechanisms of species interactions are not modeled but rather abstracted into “interspecific” effects of one species on another and “intraspecific” effects (e.g., classic Lotka-Volterra competition [Volterra 1928; MacArthur 1970, 1972], community matrices [May 1974; Pimm and Lawton 1978; Yodzis 1981; Pimm 1982], and more recent analyses [e.g., Chesson 2000; Adler et al. 2007]). In his seminal analysis, Chesson (2000) highlighted the general requirements for coexisting species to have interspecific and intraspecific density-dependent regulatory processes (i.e., stabilizing effects) that offset the level of average fitness differences among the species (i.e., equalizing effects). Adler et al. (2007) defined a stabilizing process “as any mechanism that causes species to limit themselves more than they limit others” (p. 96), and many species can simultaneously coexist if these criteria are adequately satisfied (Chesson 2000; Adler et al. 2007).

When these two approaches are contrasted, one glaring difference is the range of species that experience intraspecific density dependence. In more phenomenological models (e.g., Lotka-Volterra competition models and derivative approaches), all species experience some degree of intraspecific density dependence. In contrast, in mechanistic models of various community modules, typically the basal resources experience intraspecific density dependence, but species at higher trophic positions are regulated only through interspecific interactions. Introducing intraspecific density dependence for more species in models of community modules will undoubtedly permit more coexisting species. However, the issue is not simply to know whether more species can coexist but rather to know what are the predicted properties of these coexisting species (and by extension the properties of species that cannot coexist), what types of overall community structures are expected to result from the interplay of various intraspecific and interspecific mechanisms, and how the resulting communities might respond to major perturbations. For example, multiple consumers can coexist on a single limiting resource if those consumers also experience some degree of intraspecific density dependence (McPeck 2012). However, intraspecific density dependence in a consumer does not guarantee its place in the community. The species that can drive resources to the lowest level in isolation and the strength of intraspecific density dependence in this species set the bounds on the properties of other consumers that can potentially coexist (McPeck 2012).

In this article, I consider how the presence of a top predator influences the numbers and types of competing consumers that can coexist in models of both diamond-shaped (i.e., keystone) and intraguild predation community modules when these consumers also experience intraspecific density dependence. As expected, intraspecific

density dependence in the consumers allows many more than two consumers to coexist in these models. The presence of a top predator shifts the emphasis for coexistence from the consumer that can depress resources the most in isolation (i.e., the  $R^*$  rule; Tilman 1982; see also McPeck 2012 for the case with intraspecific density dependence) to the set of consumers that can support populations within a range of resource and predator abundances that is set by resource productivity and the predator’s own mortality rate. Moreover, major changes in consumer species richness after the addition or removal of the top predator (i.e., the “keystone predation” response [Paine 1966, 1974]) occur only when the strength of intraspecific density dependence differs greatly among the consumers and the predator inflicts greater mortality on the species with weaker intraspecific density dependence. Finally, the consequences of intraspecific density dependence under intraguild predation differ among areas of parameter space that result in point equilibria or limit cycles.

## Model and Analyses

### *Basic Model*

In this analysis, I use a modified version of the Lotka-Volterra predator-prey model as a basic framework for three trophic levels (e.g., see Holt et al. 1994; Leibold 1996; McPeck 1996; Holt and Polis 1997; Diehl and Feißel 2000; Mylius et al. 2001; Revilla 2002; Křivan and Diehl 2005; Rudolf 2007; Amarasekare 2008). Here multiple consumers ( $N_i$ )—the intraguild prey—feed on one basal resource ( $R$ ), and a generalist predator ( $P$ )—the intraguild predator—feeds on both the consumers and the basal resource. The resource and each consumer can all experience some degree of negative intraspecific density dependence in their per capita demographic rates. The full model with  $i = 1, 2, \dots, n$  consumers is

$$\begin{aligned} \frac{dR}{dt} &= R \left( c - dR - \sum_{i=1}^n a_i N_i - \varphi P \right), \\ \frac{dN_i}{dt} &= N_i [b_i a_i R - \alpha_i P - (f_i + g_i N_i)], \\ \frac{dP}{dt} &= P \left( \varphi \rho R + \sum_{i=1}^n \beta_i \alpha_i N_i - \delta \right). \end{aligned} \quad (1)$$

In this formulation,  $c$  is the maximum birth (or supply) rate of the resource, and  $d$  defines the strength of density dependence in the resource’s birth (supply) rate. The resource can be considered a biotic resource with density dependence itself or an abiotic resource that has a limiting supply (e.g., Tilman 1982). In the absence of all consumers, the resource will equilibrate at  $R^* = cd$ , where the su-

perscript asterisk denotes an equilibrium abundance. For the  $n$  consumers, each feeds on the resource according to a linear functional response, with  $a_i$  defining the attack coefficient and  $b_i$  the efficiency of converting the consumed resource into new consumers. Negative intraspecific density dependence is generated by assuming that the per capita death rate of each consumer is a linearly increasing function of its own abundance, with  $f_i$  defining the per capita death rate when the consumer is rare and  $g_i$  specifying the strength of intraspecific density dependence (i.e., the rate at which the per capita death rate increases with intraspecific density; e.g., Gilpin 1975; Gatto 1991; Caswell and Neubert 1998; Neubert et al. 2004; Amarasekare 2008; McPeck 2012). Similarly, the predator feeds on the basal resource, with parameter  $\varphi$  defining the attack coefficient and parameter  $\rho$  defining the conversion efficiency, and on each consumer with parameter  $\alpha_i$  defining the attack coefficient and parameter  $\beta_i$  defining the conversion efficiency. This model specifies a diamond-shaped module if  $\varphi = 0$  and an intraguild predation if  $\varphi > 0$ . The predator also has a per capita death rate of  $\delta$ . Consumers interact only indirectly through their feeding on the shared resource and through the shared predation they experience from the top predator. However, consumers interact with the predator via both direct mortality imposed by predation and resource competition. I will use the term “consumer” for the intraguild prey and the term “predator” for the intraguild predator to emphasize the relationships of these results among various types of community modules.

*Food Chains with Intraspecific Density Dependence*

To establish a foundation about the consequences of intraspecific density dependence across multiple trophic levels, first consider the system of isoclines for a simple food chain with only one intermediate consumer ( $n = 1$ ). With no intraspecific density dependence in the resource or the consumer ( $d = g_i = 0$ ), no three-species equilibrium exists, because the predator isocline cannot cross the intersection line of the consumer and resource isoclines unless it is coincident with the resource isocline (fig. 1A).

Introducing intraspecific density dependence to the resource ( $d > 0$ ) permits the three species to coexist at a stable equilibrium if two conditions are met:

$$\frac{c}{d} > \frac{f_1}{a_1 b_1}, \tag{2}$$

$$\frac{ca_1 b_1 - df_1}{a_1^2 b_1} > \frac{\delta}{\alpha_1 \beta_1}.$$

The first ensures that the consumer and resource can coexist in the absence of the predator. If so, the consumer

isocline and the resource isocline intersect along a line segment from the point  $[R, N_1, P] = [f_1/(a_1 b_1), (ca_1 b_1 - df_1)/(a_1^2 b_1), 0]$ , where they intersect in the  $N_1$ - $R$  face, to  $[c/d, 0, (ca_1 b_1 - df_1)/(d\alpha_1)]$ , where they intersect in the  $R$ - $P$  face (fig. 1B). The second inequality in equation (2) ensures that the predator isocline intersects this line segment and thus can sustain a population by feeding on the consumer. The point where the three isoclines intersect is a stable equilibrium (e.g., Pimm 1982), given by

$$[R_{(N_1, P)}^*, N_{1(R, P)}^*, P_{(R, N_1)}^*] = \left[ \frac{c\alpha_1 \beta_1 - a_1 \delta}{d\alpha_1 \beta_1}, \frac{\delta}{\alpha_1 \beta_1}, \frac{\alpha_1 \beta_1 (ca_1 b_1 - df_1) - a_1^2 b_1 \delta}{a_1^2 \alpha_1 \beta_1} \right] \tag{3}$$

(the parenthetical subscripts identify which other species are present at this equilibrium).

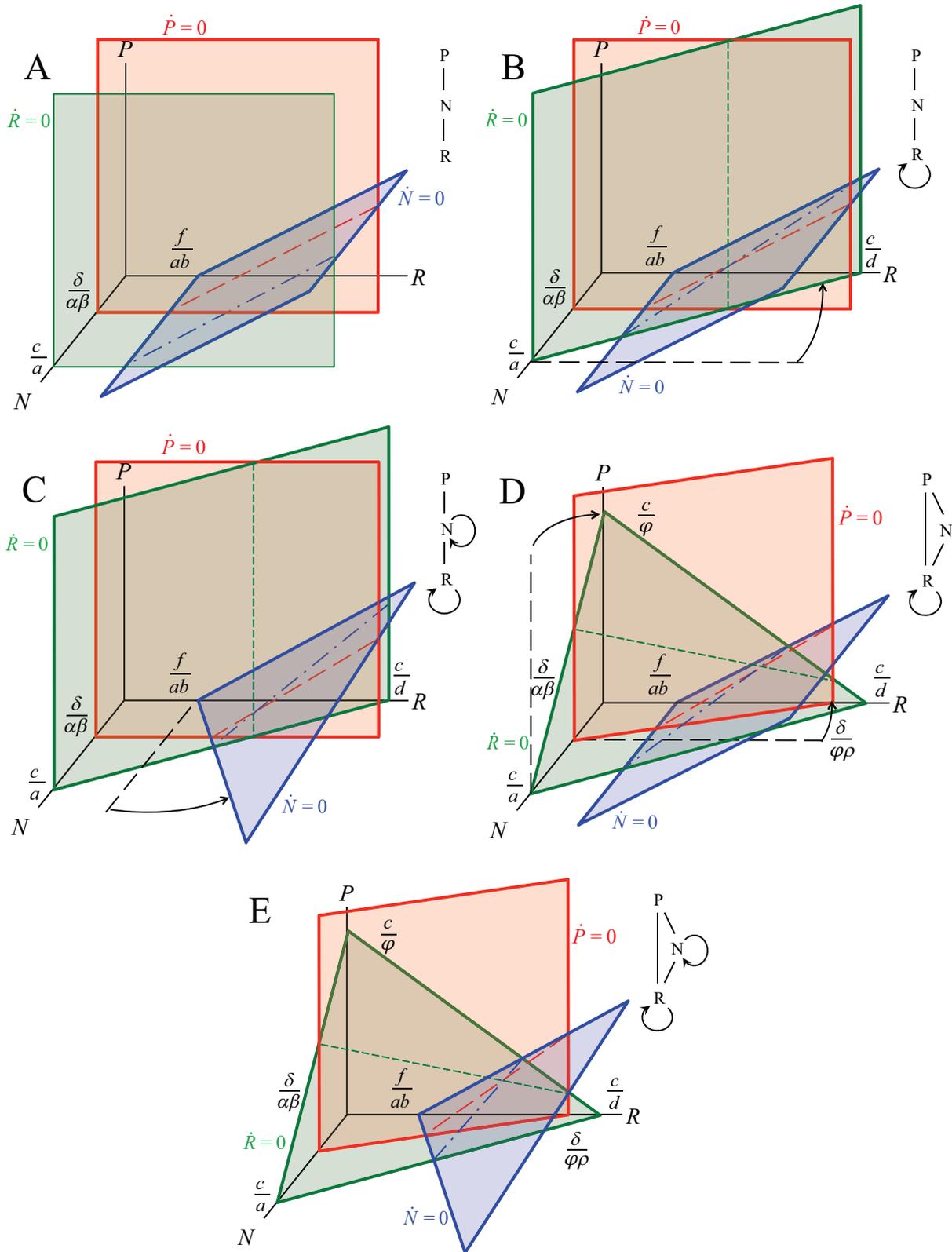
Adding intraspecific density dependence to the consumer ( $g_i > 0$ ) changes the shape of the consumer isocline (fig. 1C). The consumer isocline still intersects the  $R$ -axis at  $f_1/(a_1 b_1)$ , which defines the lowest resource abundance at which the consumer still has a positive population growth rate in the absence of the predator and still has a slope of  $a_i b_i / \alpha_i$  in the  $R$ - $P$  face. However, the consumer isocline is now not parallel to the  $N_1$ -axis: the slope of the consumer isocline in the  $N_1$ - $R$  face is now  $a_i b_i / g_i$  instead of  $\infty$  (cf. fig. 1B, 1C), and this subtle difference is what will permit more than two coexisting consumers (see below). Increasing the strength of the consumer’s intraspecific density dependence reduces the predator’s abundance but leaves the consumer’s abundance and the resource’s abundance unchanged, such that

$$[R_{(N_1, P)}^*, N_{1(R, P)}^*, P_{(R, N_1)}^*] = \left[ \frac{c\alpha_1 \beta_1 - a_1 \delta}{d\alpha_1 \beta_1}, \frac{\delta}{\alpha_1 \beta_1}, \frac{\alpha_1 \beta_1 (ca_1 b_1 - df_1) - a_1^2 b_1 \delta - g_i \delta}{a_1^2 \alpha_1 \beta_1} \right]. \tag{4}$$

*Diamond-Shaped Community Module*

*No Consumer Intraspecific Density Dependence.* Now consider whether multiple consumers can be added to the linear food chain to form a diamond-shaped community module. The diamond-shaped community module has multiple intermediate-trophic-level consumers, but the top predator does not feed on the basal resource.

With no intraspecific density dependence in the consumers (i.e., all  $g_i = 0$ ), at most two consumers can coexist when competing for a shared resource and being fed upon by a shared predator (see also Holt et al. 1994; Leibold 1996; McPeck 1996). To see why, first consider the con-



E4

sumer isoclines. In this case, all consumer isoclines are independent of their own abundances and the abundances of all other consumers. Thus, all other dimensions besides  $R$  and  $P$  are irrelevant to determining whether the isoclines of two consumers intersect (fig. 2). For two consumer isoclines to intersect, the isocline that intersects the  $R$ -axis at the lower  $f_i/(a_i b_i)$  must have the shallower isocline slope  $a_i b_i/\alpha_i$  in the  $R$ - $P$  face (fig. 2). This defines one criterion for the four species to coexist as

$$\frac{\alpha_1}{\alpha_2} > \frac{a_1 b_1}{a_2 b_2} > \frac{f_1}{f_2} \tag{5}$$

(see also Leibold 1996). The intersection of the consumer isoclines fixes the resource and predator abundances, respectively, at

$$R_{(N_1, N_2, P)}^* = \frac{\alpha_2 f_1 - \alpha_1 f_2}{a_1 b_1 \alpha_2 - a_2 b_2 \alpha_1}, \tag{6}$$

$$P_{(R, N_1, N_2)}^* = \frac{a_2 b_2 f_1 - a_1 b_1 f_2}{a_1 b_1 \alpha_2 - a_2 b_2 \alpha_1}$$

(e.g., Leibold 1996). Otherwise, the species with the lowest  $f_i/(a_i b_i)$ , and therefore with its entire isocline above all other isoclines for all values of  $R$  in the  $R$ - $P$  face, can drive all other consumers to extinction and will exist alone at the intermediate trophic level of this food chain.

The other criterion for coexistence of the two consumers is

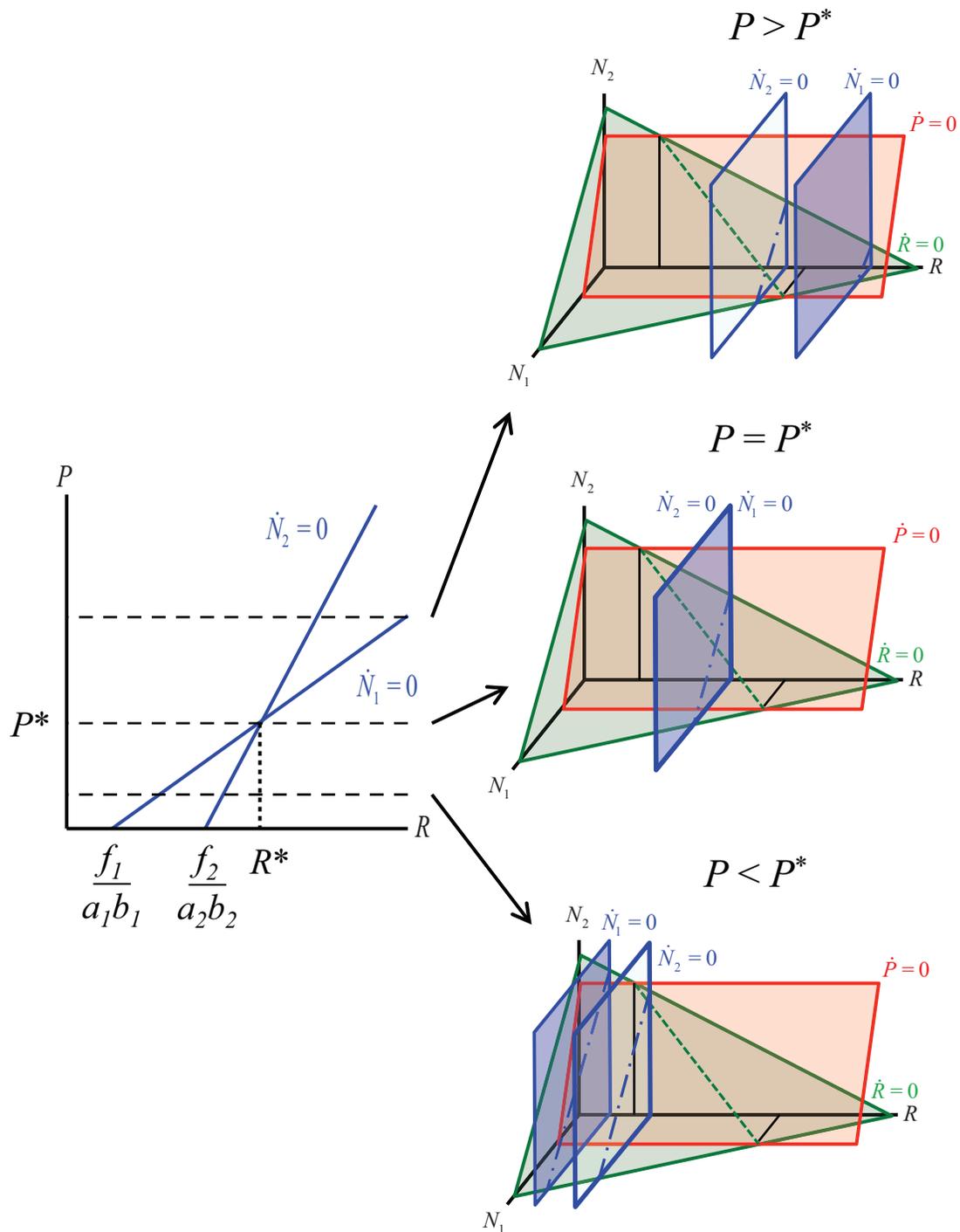
$$\frac{\alpha_1 \beta_1}{a_1} > \frac{\delta}{c - dR^*} > \frac{\alpha_2 \beta_2}{a_2}, \tag{7}$$

which ensures that the predator isocline and the resource isocline also cross at the intersection of the consumer isoclines (see also Leibold 1996). The full four-dimensional representation of the isoclines cannot be made for these four species, but the problem can be adequately understood by considering the four isoclines in the  $R$ - $N_1$ - $N_2$  subspace (fig. 2). The resource and predator isoclines intersect along a line that proceeds from  $[R, N_1, N_2] = [(c\alpha_2\beta_2 - a_2\delta)/(d\alpha_2\beta_2), 0, \delta/(\alpha_2\beta_2)]$  to  $[(c\alpha_1\beta_1 - a_1\delta)/(d\alpha_1\beta_1), \delta/(\alpha_1\beta_1), 0]$  (i.e., the green dashed line in the three-dimensional [3-D] panels of fig. 2; note that the nonzero abundances at the

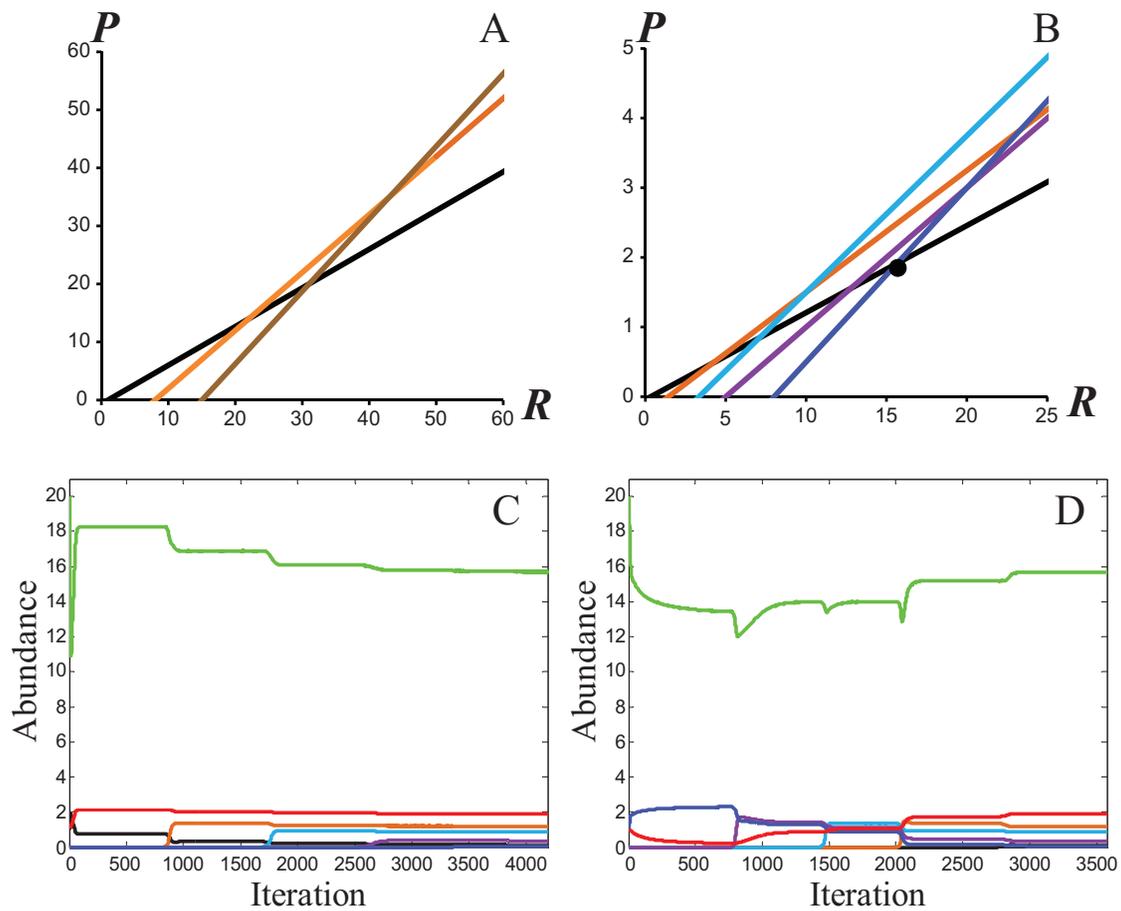
endpoints of this line segment are the equilibrium resource and consumer abundances for the respective food chains containing the resource, the predator, and the respective consumer). Because the resource isocline and the predator isocline are independent of the predator abundances, their positions in this 3-D space do not change as predator abundance changes. However, the positions of the two consumer isoclines do change depending on the value of  $P$ . Each consumer's isocline is a plane that is parallel to all consumer axes, and its position on the  $R$ -axis is given by  $R = f_i/(a_i b_i) + \alpha_i P$ . At  $P = 0$ , the two isoclines are at their respective  $f_i/(a_i b_i)$  values, and as  $P$  increases, the isoclines move to larger values of  $R$  (i.e., to the right along the  $R$ -axis in the 3-D panels of fig. 2). If the consumer with the lower  $f_i/(a_i b_i)$  has the larger  $\alpha_i$ , then the two consumer isoclines will be coincident (i.e., they intersect in this subspace) at one  $R$  value (note that this implies a trade-off such that the better resource competitor also experiences disproportionate mortality from the predator [Holt et al. 1994; Leibold 1996; McPeck 1996]). The point where the two consumer isoclines are coincident corresponds to the point where the two consumer isoclines cross in the  $R$ - $P$  subspace (fig. 2). If this  $R$  value occurs somewhere in the range where the  $R$  and  $P$  isoclines intersect, then this defines the position of the four-species equilibrium (fig. 2), and this point equilibrium is stable (Holt et al. 1994; Leibold 1996). However, if this point of consumer isocline coincidence occurs outside the range of  $R$ - $P$  intersection, only one of the consumers can coexist with the resource and predator.

In the absence of the predator, the consumer with the lowest value for  $f_i/(a_i b_i)$  will drive all others to extinction because it can depress the resource level to the lowest value, namely to  $f_i/(a_i b_i)$  (i.e., the  $R^*$  rule; Tilman 1982). However, when the predator is present, the  $R^*$  rule does not apply to the consumers. For example, consider the three consumer isoclines illustrated in the  $R$ - $P$  face in figure 3A. Assuming that all other parameters are fixed (parameter values for this illustration are given in the legend of fig. 3A), which consumers will coexist depends on the productivity of the resource (i.e.,  $c$ ) and the mortality rate of the predator (i.e.,  $\delta$ ; see eq. [7]). Increasing values of  $c$  cause the points of intersection of the resource isocline to

**Figure 1:** Isocline diagrams for five trophic-level food chains in which different species experience intraspecific density dependence. For the three food chains, intraspecific density dependence is present in no species (A), in the resource (B), and in the resource and the consumer (C). D, E, Shifts in isoclines when the top predator also feeds on the basal resource (i.e., intraguild predation), with only the basal resource (D) and both the consumer and the basal resource (E) experiencing intraspecific density dependence. In each panel, the green plane represents the isocline of the basal resource (R), the blue plane represents the isocline of the intermediate-trophic-level consumer (N), and the red plane represents the isocline of the top predator (P). The blue dot-dashed line identifies the intersection between the resource isocline and the consumer isocline, the red dashed line identifies the intersection between the consumer isocline and the predator isocline, and the green dashed line identifies the intersection between the resource isocline and the predator isocline. The values where the various isoclines intersect the axes are labeled. The black dashed lines and arrows illustrate how various isoclines shift positions with increasing levels of intraspecific density dependence and the addition of intraguild predation.



**Figure 2:** Various representations of the isocline system for a resource, two consumers ( $N_1$  and  $N_2$ ), and a predator in the diamond-shaped community module with no consumer intraspecific density dependence. The two-dimensional graph on the left shows the relationship between the two consumer isoclines needed for their coexistence. The three three-dimensional graphs on the right illustrate the isoclines for the four species in the  $R$ - $N_1$ - $N_2$  subspace for different values of the predator abundance. The positions of the resource isocline and the predator isocline do not change, but the positions of the two consumer isoclines move to larger  $R$  values as  $P$  increases. The two consumer isoclines are coincident at only one  $P$  value, and this defines the four-species equilibrium.



**Figure 3:** Consumer isoclines for multiple species when consumers experience no intraspecific density dependence (A) or do experience intraspecific density dependence (B). A, The isoclines for three consumers. Because the lines of intersection between these planes are parallel to all consumer axes, the information about the isoclines in the  $R$ - $P$  face (i.e., the plane through the  $R$ - $P$  dimensions where all  $N_i = 0$ ) shows all relevant aspects of this scenario. The black line isocline represents consumer 1, the orange isocline represents consumer 2, and the brown isocline represents consumer 3. All consumers have  $a_i = 1$ ,  $b_i = \beta_i = 0.1$ , and  $g_i = 0$ . Other parameters for the consumers are  $f_1 = 0.1$  and  $\alpha_1 = 0.15$ ,  $f_2 = 0.8$  and  $\alpha_2 = 0.1$ , and  $f_3 = 1.5$  and  $\alpha_3 = 0.8$ . The resource has  $d = 0.2$ , and the predator has  $\delta = 0.1$ . Which of these consumers will coexist depends on the productivity of the resource (i.e., the value of  $c$ ; see text for details). B, The isoclines of five consumers in the  $R$ - $P$  face that coexist at a stable point equilibrium in a keystone predation community module because of intraspecific density dependence in the consumers. Parameter values used for this example are as follows: resource  $c = 5.0$ ,  $d = 0.2$ ; predator  $\delta = 0.1$ ; black consumer  $f = 0.05$ ,  $g = 0.2$ ,  $a = 1.5$ ,  $b = 0.1$ ,  $\alpha = 1.2$ ,  $\beta = 0.1$ ; orange consumer  $f = 0.1$ ,  $g = 0.2$ ,  $a = 0.7$ ,  $b = 0.1$ ,  $\alpha = 0.4$ ,  $\beta = 0.1$ ; light blue consumer  $f = 0.15$ ,  $g = 0.2$ ,  $a = 0.45$ ,  $b = 0.1$ ,  $\alpha = 0.2$ ,  $\beta = 0.1$ ; lavender consumer  $f = 0.3$ ,  $g = 0.1$ ,  $a = 0.6$ ,  $b = 0.1$ ,  $\alpha = 0.3$ ,  $\beta = 0.1$ ; and dark blue consumer  $f = 0.8$ ,  $g = 0.1$ ,  $a = 1.0$ ,  $b = 0.1$ ,  $\alpha = 0.4$ ,  $\beta = 0.1$ . The filled dot identifies the equilibrium value for the resource and predator at values of  $[R^* = 15.7, P^* = 1.9]$ , and note that all the consumer isoclines pass above this point (some only slightly above). C, The species abundances for serial introductions of the five consumers in B. The abundances of the resource (green line), the top predator (red line), and five consumers (line colors same as isoclines in B) are shown from numerical simulations. D, The serial introduction of the same consumers but in reverse order. Matlab code for simulating up to five consumers is given in the appendix, available online.

increase on all three axes in the 3-D panels of figure 2. As a result, the line of intersection between the resource isocline and the predator isocline moves to a larger range of  $R$  (and thus  $P$ ) values. For the consumers depicted in figure 3A to have enough resource productivity to support the predator, it is required that  $c > 6.87$  (i.e., the lowest value of  $c$  at which the predator can support a population on

the solid-line consumer, which depends on the second inequality given in eq. [2]). Only consumer 1 will be present as  $c$  is increased further, until  $c = 11.6$ . At this value of  $c$ , the highest point of intersection between the  $R$  isocline and the  $P$  isocline is now coincident with the  $R$  value at which the two consumer isoclines are coincident. As  $c$  is increased further,  $N_2$  will increase and  $N_1$  will decrease,

until the lowest point of intersection between the  $R$  isocline and the  $P$  isocline passes the coincident consumer planes, at which point  $N_1$  will become extinct. As  $c$  is increased even further, the same series of consumer coexistence and replacement with  $N_2$  and  $N_3$  will occur. Similar results are obtained by increasing  $\delta$ , which shifts the predator isocline to higher values on the consumer isoclines but does not alter the position of the other isoclines.

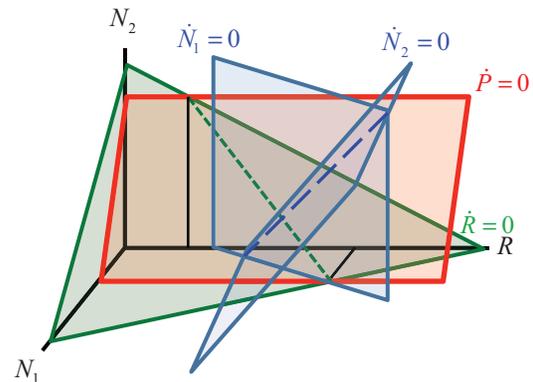
*Adding Consumer Intraspecific Density Dependence.* Now permit all consumers to experience some level of intraspecific density dependence (i.e.,  $g_i \geq 0$ ). Remember that with only one consumer present, the resource equilibrates at the same abundance as when  $g_i = 0$ , but the predator equilibrates at a lower abundance (cf.  $P^*$  in eqq. [3], [4]). Consumer intraspecific density dependence, therefore, reduces the predator abundance for a given resource abundance at which other consumers must have a positive population growth rate to invade. Because the consumer isoclines are now not constrained to intersect in the  $R$ - $P$  face, the isoclines of many more than two consumers can possibly intersect to result in a community with multiple consumers present. The number of nonindependent dimensions to this problem makes graphically representing the process difficult. Moreover, the equations for the equilibrium abundances of the species are complicated functions of parameters from all the other species in the system and are not useful in illuminating the process. However, we can think through what each successive consumer must be able to achieve to successfully invade the community and what the consequences of that invasion will be.

First, consider how the various isoclines change with intraspecific density dependence in multiple dimensions for only two consumers. The shapes and the positions of the resource isocline and the predator isocline are unchanged, but each consumer isocline now angles away from its own axis (fig. 4). As the consumer isoclines consequently slide along the  $R$ -axis as  $P$  is changed in figure 4, the consumer isoclines now will intersect across a wide range of  $P$  values and, hence,  $R$  values, instead of at only a single point (cf. figs. 2, 4). Thus, many consumer isoclines can all intersect simultaneously at given values of  $R$  and  $P$ .

With one consumer present, the system will rapidly come to its three-species equilibrium, which will set values for  $R_1^*$  and  $P_1^*$  (where the subscript I denotes that one consumer is present; fig. 1C). For a second consumer to invade this community, it must have a positive population growth rate at the following resource and predator abundances when the second consumer is rare:

$$a_i b_i R_1^* > \alpha_i P_1^* + f_i. \quad (8)$$

In other words, its isocline must pass above this point in



**Figure 4:** The isocline system in the  $R$ - $N_1$ - $N_2$  subspace for a system with two consumers that both experience intraspecific density dependence. The color patterns and symbols are as defined in figures 1 and 2. Compare this figure with figure 2. With consumer intraspecific density dependence, the consumer isoclines intersect (blue dashed line) over a wide range of  $R$  and  $P$  values.

the  $R$ - $P$  face (i.e., where its abundance is 0). To do this, the consumer's isocline must intersect the  $R$ -axis below  $R_1^*$  (i.e.,  $f_i/(a_i b_i) < R_1^*$ ), and its slope ( $a_i b_i/\alpha_i$ ) must be sufficiently steep to pass above the point. If this is true, the second consumer will increase in abundance as the community comes to a new equilibrium. As a consequence, the resource and the predator will both increase or decrease (call their new abundances  $R_{II}^*$  and  $P_{II}^*$ , respectively; fig. 3C, 3D). To see why, note that the intersection between the resource isocline and the consumer isocline defines a positive relationship between the equilibrium abundances of the predator and the resource (fig. 1C). However, for the consumer already present, its abundance may increase or decrease depending on the combined change in resource and predator abundances.

For a third consumer to invade, its isocline must pass above the new point of resource and predator equilibrium abundances [ $R_{II}^*$ ,  $P_{II}^*$ ] in the  $R$ - $P$  face. If true, this consumer will increase in abundance, and the resource and predator abundances will decrease further; the abundances of the other consumers may increase or decrease. A sequence of consumer invasions will continue until no other consumer has an isocline that passes above the resulting resource-predator abundance combination in the  $R$ - $P$  face for the consumers already present. Also, as one consumer invades, other consumers may become extinct because resource and predator abundances decrease to a point where these consumers cannot support a population. Extensive simulations indicate that the system always arrives at a stable equilibrium (code given in appendix, available online).<sup>1</sup>

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

Any number of consumers can invade and coexist, if they all can mutually invade the system with all other consumers present. Figure 3B presents the  $R$ - $P$  face for a system in which five consumers coexist (the parameter values for each species are given in the legend). If none of the consumers experienced intraspecific density dependence (i.e., all  $g_i = 0$ ), then only the consumer with the light blue isocline (i.e., the middle value for  $f_i/(a_i b_i)$ ) would coexist with the resource and predator. With all  $g_i > 0$ , these five consumers coexist (fig. 3B). One can imagine many other consumers that could invade and coexist in this example, but these five make the point. It is impossible to specify definitive criteria for the characteristics of the consumers that will coexist, other than that they will all have  $f_i/(a_i b_i)$  less than the equilibrium resource abundance and their isoclines will all pass above the resource-predator combination in the  $R$ - $P$  face. Their isoclines need not have any particular pattern of crossing in this multidimensional state space.

*Keystone Predation.* The full concept of keystone predation includes not only the coexistence of multiple consumers that are all competing for a shared resource while being fed upon by a shared predator (i.e., a diamond-shaped community module) but also the predator that is preventing resource monopolization by one of the consumers (Paine 1966, 1974). In other words, one consumer will drive all others to extinction in the absence of the predator. What combinations of parameter values are required for this to occur?

If the species with the lowest  $f_i/(a_i b_i)$  also experiences substantially less intraspecific density dependence than the other consumers, then it will drive all other consumers to extinction in the absence of the predator (McPeck 2012). Consider again the consumers depicted in figure 3B. If intraspecific density dependence is greatly reduced or removed from the consumer with the isocline represented by the black line (i.e., setting  $g < 0.04$ ), then this consumer in the absence of the predator will drive the other four to extinction, because it can depress resources to a level at which no other consumer can support a population (Tilman 1982; McPeck 2012). However, all five consumers still coexist at abundances that are only slightly changed (as compared to when they experience comparable levels of intraspecific density dependence) when the predator is present in the community. A greater range of consumers can also coexist with the predator if the predator has a higher attack rate on the consumer that can drive all others extinct in its absence.

In contrast, if all consumers experience similar levels of intraspecific density dependence, removing the predator will have less effect on the coexisting consumers. For example, again for the consumers depicted in figure 2B,

removing the predator causes the two consumers with the highest  $f_i/(a_i b_i)$  to become extinct but the other three to coexist. If the predator has relatively similar attack rates on all the consumers, typically very few consumers are lost when the predator is removed because the relative demographic performances among the consumers are unchanged.

### Intraguild Predation

*No Consumer Intraspecific Density Dependence.* With no intraspecific density dependence in the consumers, intraguild predation (i.e., the top predator also consumes the basal resource) alters the isoclines of the typical linear, three-trophic-level-community module in two ways (fig. 1D). First, the resource isocline intersects all three axes: it intersects the  $R$ -axis at  $c/d$ , the  $N$ -axis at  $c/a_1$ , and the  $P$ -axis at  $c/\varphi$ . Also, because the predator consumes the resource, the predator isocline intersects the  $R$ -axis at  $\delta/(\varphi\rho)$ . Consumer isoclines are unaffected by the addition of the predator feeding on the resource.

An equilibrium having the predator, consumer, and resource all at positive abundances will exist if a number of criteria are met (Holt and Polis 1997; Diehl and Feißel 2000; Mylius et al. 2001; Revilla 2002; Krivan and Diehl 2005). Again, the consumer isocline must intersect the  $R$ -axis at a value that is lower than the equilibrium abundance of the resource in the absence of both the consumer and predator:

$$\frac{f}{ab} < \frac{c}{d}, \tag{9}$$

which ensures that the consumer can coexist with the resource in the absence of the predator (fig. 1D). If this inequality is satisfied, then the consumer isocline and the resource isocline will intersect along a line from the point  $[R, N, P] = [(c\alpha + f\varphi)/(ab\varphi + d\alpha), 0, (cab - df)/(ab\varphi + d\alpha)]$  in the  $P$ - $R$  face to  $[f/(ab), (cab - df)/(a^2b), 0]$  in the  $R$ - $N$  face. For the three-species equilibrium to exist, the predator isocline must intersect this line. For this to occur,

$$\frac{\delta}{\varphi\rho} > \frac{c\alpha + f\varphi}{ab\varphi + d\alpha}, \tag{10}$$

which ensures that the predator isocline intersects the  $R$ -axis above the resource level where the resource and consumer isoclines intersect (fig. 1A). Inequality (10) thus ensures that the predator cannot depress the resource to a level at which the consumer cannot maintain a viable population (see also Holt and Polis 1997); in other words, the consumer is a better resource competitor than the predator. The other criterion is

$$\frac{\delta}{a} \left( \frac{cab - df}{\delta ab - f\varphi\rho} \right) > \frac{\delta}{\alpha\beta}, \quad (11)$$

which ensures that the predator isocline intersects the  $N$ -axis at a level where the combined resource and consumer populations can support a predator population. If  $\delta/(\varphi\rho) > c/d$ , then the predator cannot support a population on the resource alone. However, feeding on the resource permits the predator to persist at a consumer abundance that would not be possible if its diet were not supplemented by the resource:

$$\frac{\delta}{a} \left( \frac{cab - df}{\delta ab - f\varphi\rho} \right) > \frac{\delta}{\alpha\beta} > \frac{cab - df}{a^2b}. \quad (12)$$

This three-species equilibrium is stable over much of parameter space, but areas exist where the three species cycle (Holt and Polis 1997; Křivan and Diehl 2005; Tanabe and Namba 2005).

Can multiple consumers (i.e., intraguild prey) coexist with the predator in the absence of consumer intraspecific density dependence? To examine this, first consider the introduction of a second consumer. The consumer isoclines in this case are unchanged from the situation in which the predator does not consume the resource (see fig. 5). Thus, although the predator eats the resource, both the predator and the resource equilibrate at the same abundances as in the diamond-shaped community module (i.e., eq. [6]). Also, note that as with the diamond-shaped module, this implies that at most two consumers can coexist under intraguild predation with no intraspecific density dependence in the consumers if a stable equilibrium results.

As with the diamond-shaped module, this determines the resource abundance at which the consumer isoclines are coincident in the  $R$ - $N_1$ - $N_2$  subspace, but the conditions under which this will result in both consumers coexisting with the predator are more stringent. In the  $R$ - $N_1$ - $N_2$  subspace, the predator isocline is independent of the predator's abundance (fig. 5). However, the resource isocline intersects each axis at progressively lower points as predator abundance increases; these points are given by  $R = cd - P\varphi/d$ ,  $N_1 = ca_1 - P\varphi/a_1$ , and  $N_2 = ca_2 - P\varphi/a_2$ . As  $P$  is increased, the consumer isoclines slide to higher values of  $R$  just as with the diamond-shaped module, but the line of intersection between the consumer isocline and the predator isocline decreases because of the movement of the resource isocline as  $P$  increases. Again, for the four species to coexist, the consumer isoclines must be coincident when they also intersect the line of intersection between the consumer isocline and the predator isocline (fig. 5).

The above results are true only in areas of parameter space in which a stable equilibrium results. In areas of

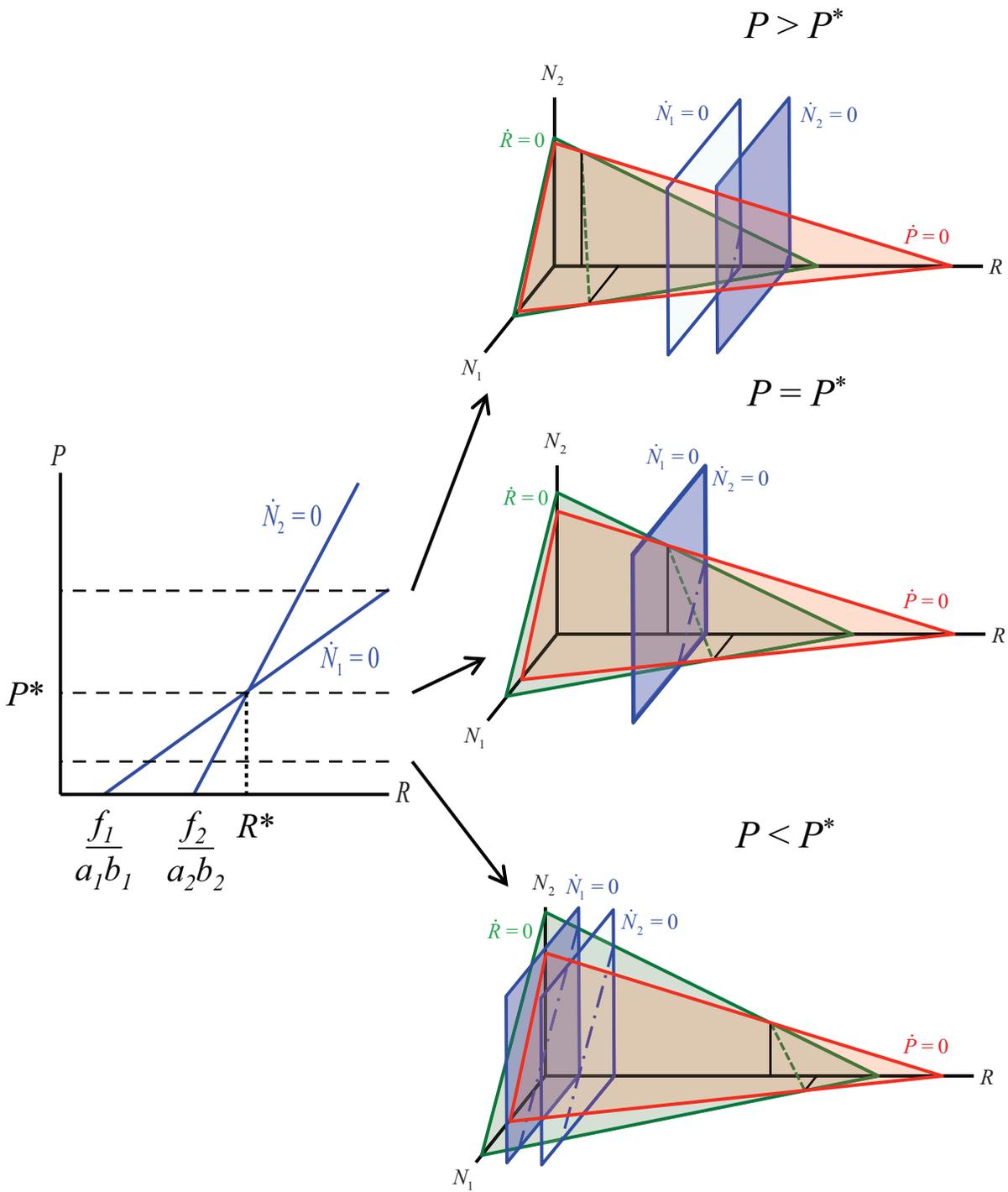
parameter space in which cycles result, more than two consumers can coexist. For example, figure 6A illustrates a case in which four consumers coexist with an intraguild predator. All four consumers cycle in phase with one another and lag behind the resource by one-quarter phase, and the predator cycles lag behind the consumers by one-quarter phase.

*Adding Consumer Intraspecific Density Dependence.* Adding consumer intraspecific density dependence to the intraguild prey has different effects on consumer species richness depending on whether the system is cycling or at a stable equilibrium. The full isocline system for one intraguild prey is given in figure 1E. In areas of parameter space where cycles result in its absence, adding intraspecific density dependence to the consumer with the lowest  $f_i/(a_i b_i)$  stops the cycles (cf. fig. 6A, 6B). However, adding intraspecific density dependence to any other consumer does not stop the cycling, and so more than two consumers will remain cycling in the system (fig. 6C).

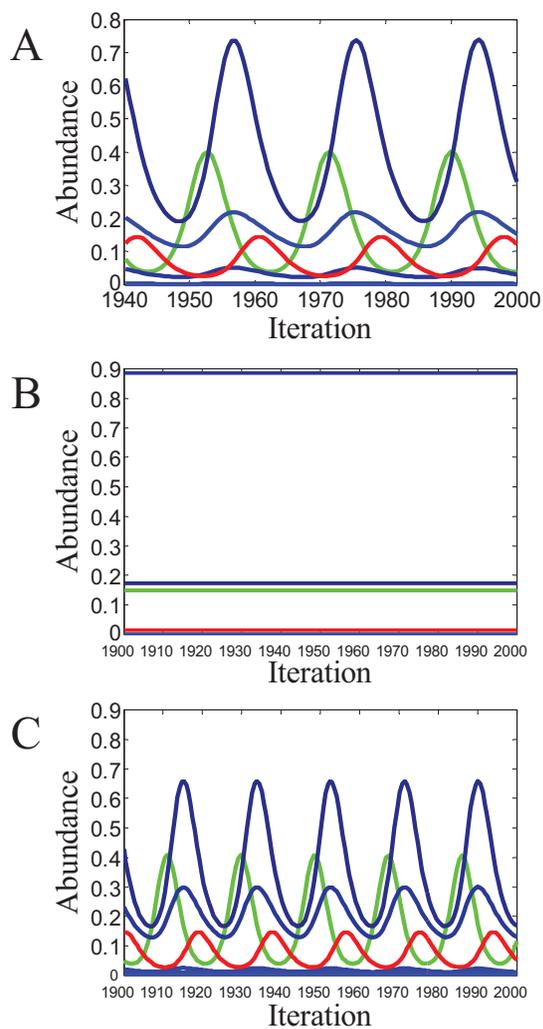
In contrast, in areas of parameter space where a stable equilibrium results in its absence, intraspecific density dependence in the consumers allows more than two consumers to coexist in the intraguild predation module. Remember that the shapes of the consumer isoclines are unaffected by intraguild predation. However, the predator feeding on the resource makes the criteria for the coexistence of more than two consumers more stringent than in the diamond-shaped module lacking intraguild predation (analogous to what is illustrated in fig. 3). For example, increasing the attack coefficient of the predator on the resource (i.e.,  $\varphi$ ) increases the equilibrium abundances of both the predator and the resource, but the predator abundance increases faster than the resource abundance with increasing  $\varphi$ . Consequently, fewer consumers can meet the criteria for invasion, and the abundances of coexisting consumers are lower than in the absence of intraguild predation. Interestingly, the keystone predation effect still holds under intraguild predation just as in the diamond-shaped module, if the intraguild prey with the lowest  $f_i/(a_i b_i)$  also experiences substantially lower intraspecific density dependence than the other consumers and if the intraguild predator imposes substantially more mortality on this consumer than the other consumers.

## Discussion

Phenomenological models of coexistence have suggested important insights, but they may be inadequate to provide understanding about how various types of processes interact to permit species to live together. In his seminal synthesis, Chesson (2000) identified two critical components needed to understand species coexistence: (1) the



**Figure 5:** Various representations of the isocline system for a resource, two consumers ( $N_1$  and  $N_2$ ), and a predator in the intraguild predation community module with no consumer intraspecific density dependence. The two-dimensional graph on the left shows the relationship between the two consumer isoclines needed for their coexistence. The three three-dimensional graphs on the right illustrate the isoclines for the four species in the  $R$ - $N_1$ - $N_2$  subspace for different values of the predator abundance. The position of the predator isocline does not change. However, the resource isocline intersects each axis at progressively lower points as predator abundance increases. Also, the positions of the two consumer isoclines move to larger  $R$  values as  $P$  increases. The two consumer isoclines are coincident at only one  $P$  value, and this defines the four-species equilibrium if they also cross the line of intersection between the resource isocline and the predator isocline.



**Figure 6:** Cycles resulting from an intraguild predation community module in which four consumers coexist with the basal resource and the intraguild predator. The abundances of the resource (green line), the intraguild predator (red line), and four consumers (intraguild prey; blue lines) are shown from numerical simulations (Matlab code given in the appendix, available online). In the simulation shown in A, parameters are  $c = 1.0$ ,  $d = 1.0$ ; predator:  $\delta = 0.5$ ,  $\varphi = 4.0$ ,  $\rho = 0.1$ ; consumer cycling at highest abundance:  $f = 0.1$ ,  $g = 0.0$ ,  $a = 1.0$ ,  $b = 1.0$ ,  $\alpha = 1.0$ ,  $\beta = 1.0$ ; consumer cycling at second-highest abundance:  $f = 0.1$ ,  $g = 0.0$ ,  $a = 0.6$ ,  $b = 1.0$ ,  $\alpha = 0.05$ ,  $\beta = 1.0$ ; consumer cycling at third-highest abundance:  $f = 0.1$ ,  $g = 0.0$ ,  $a = 0.7$ ,  $b = 1.0$ ,  $\alpha = 0.3$ ,  $\beta = 1.0$ ; consumer cycling at lowest abundance:  $f = 0.1$ ,  $g = 0.0$ ,  $a = 0.65$ ,  $b = 1.0$ ,  $\alpha = 0.2$ ,  $\beta = 1.0$ . In B, intraspecific density dependence is added to the highest cycling consumer from A (this consumer has the lowest  $f_i/(a_i b_i)$ ) by setting  $g = 0.2$ , but all other consumers remain with  $g = 0.0$ ; the cycling stops, and only the consumers cycling at the highest and third-highest abundances in A coexist at a stable equilibrium. In C, intraspecific density dependence in the second-highest cycling consumer in A is instead set to  $g = 0.2$ , but all other consumers have  $g = 0.0$ ; all four consumers remain cycling in the system but around different abundances and at a different frequency.

average fitness differences among species and (2) the density-dependent mechanisms that overcome these fitness differences to cause each species to limit its own abundance more than the effect each has on other species. However, the relevance and validity of this approach in the context of communities with trophic interactions, where species can influence others' abundances both directly and indirectly via effects that propagate through a web of species interactions, has always been unclear. For example, two intermediate-trophic-level consumers can coexist in a diamond-shaped community module without either having any density-dependent effects on their own abundances (Levin 1970; Holt et al. 1994; Leibold 1996; McPeck 1996). How are we to apply the axiom that species must limit their own abundances more than they limit the abundances of other species to this situation?

Understanding how the interplay of various mechanisms of species interactions fosters coexistence and shapes community structure is critical because intuition about how a process works may not stand quantitative scrutiny (e.g., Chesson and Huntly 1997) and phenomenological models may not capture critical features of mechanisms or their interactions (e.g., Tilman 1987). How intraspecific density dependence permits greater numbers of coexisting species in mechanistic models of community modules is an object lesson in why a much more nuanced and rigorous understanding is needed. In the absence of a top predator (i.e., when  $P = 0$  here), the consumers that are able to coexist with one another must be similar to one another in average fitness, but they must be similar in a particular way (McPeck 2012). Namely, the species with the lowest  $f_i/(a_i b_i)$  sets the maximum bound on the possible  $f_i/(a_i b_i)$  values for the species that might coexist, based on the strength of intraspecific density dependence in this species (McPeck 2012). In addition, intraspecific density dependence does permit more than one consumer to coexist, but not because each limits its own abundance more than it affects other species. Rather, intraspecific density dependence prevents the consumer with the lowest  $f_i/(a_i b_i)$  from monopolizing the resource. Thus, the first prediction derived from this analysis is that with intraspecific density dependence, each consumer equilibrates at an abundance above the resource level at which it could minimally maintain a positive population growth rate. Consequently, resources remain to be exploited by other consumers (McPeck 2012). Mathematically, this is manifested in the consumer isoclines not being parallel to their own axes (fig. 1C).

When the top predator is permitted into the system, a second prediction is that the focus shifts from the consumer with the lowest  $f_i/(a_i b_i)$  to the consumers that can support populations within the bounds of resource and predator abundances defined by the productivity of the

basal resource and the mortality rate of the top predator (i.e., figs. 2, 5). The predator with the lowest  $f_i/(a_i b_i)$  may not necessarily be present, and consumers are predicted to show species replacements along gradients of resource productivity or predator mortality. Here again, species must be similar to coexist, but their similarity is defined by having isoclines that cross other consumers' isoclines within these bounds (fig. 4). With intraspecific density dependence, the isoclines of two consumers can intersect over a broad range of resource and consumer abundances (e.g., figs. 2, 4, 5), and many other consumers can have isoclines that can pass through this intersection and thus potentially coexist with one another. Also, multiple consumers can coexist in this range, but here the effect of intraspecific density dependence is to determine the degree to which each consumer limits the predator abundance for a given resource level (cf. eqq. [3], [4]).

Previous theoretical analyses of intraguild predation have focused almost exclusively on the conditions permitting coexistence of one intraguild predator and one intraguild prey (e.g., Holt and Polis 1997; Diehl and Feiel 2000; Mylius et al. 2001; Revilla 2002; Křivan and Diehl 2005; Rudolf 2007; Amarasekare 2008; Schellenkens and van Kooten 2012), and so this analysis greatly extends these previous explorations by considering the conditions under which more than one intraguild prey can coexist. This analysis also synthesizes the diamond-shaped and intraguild predation community modules by showing that the same issues qualitatively determine the number of coexisting consumers both with and without the top predator being able to eat the basal resource. However, the criteria for coexistence with intraguild predation are quantitatively more stringent (cf. figs. 2, 5), and intraguild predation opens the possibility of multiple consumers coexisting even in the absence of intraspecific density dependence if the system cycles (fig. 6).

Another important implication of this analysis is that the mere existence of a top predator feeding on a set of resource competitors does not necessarily imply that the full implications of keystone predation (i.e., removal of the predator will result in a great reduction in consumer species richness [Paine 1966, 1974]) will be manifest. If all consumers experience significant and similar strengths of intraspecific density dependence, then removing the predator may simply cause alterations in consumer abundances, with few consumers being driven to extinction as a consequence (McPeck 2012). Extensive explorations of parameter space with this model suggest that the outcome associated with keystone predation is much more prevalent when two conditions hold: the consumer in the community that can support a population at the lowest resource level (i.e., the one with the lowest  $f_i/(a_i b_i)$  of the coexisting consumers) experiences substantially lower lev-

els of intraspecific density dependence than other consumers, and the predator has a biased consumption for the consumer with the lowest  $f_i/(a_i b_i)$ . Moreover, the keystone predation effect results both with and without intraguild predation.

This analysis, therefore, suggests strong, testable predictions for real systems about keystone predation and community structure in diamond-shaped and intraguild predation modules. Predator removal will significantly reduce consumer species richness in systems where the consumer assemblage has specific features. Those features are that the consumers that can have positive population growth rates at the lowest resource abundance also experience substantially weaker intraspecific density dependence than the other consumers, and that predator foraging is biased toward these consumers. Note that these features also imply the same trade-off between competitive ability and predation risk as in the original formulations of diamond-shaped community modules (Levin 1970; Holt et al. 1994; Leibold 1996), with the added condition that superior resource competitive ability also includes lower levels of intraspecific density dependence (McPeck 2012). However, removing the top predator will not result in a substantial reduction in consumer species richness in every system. Specifically, predator removal will have little effect on consumer richness if the consumers all experience significant but relatively similar levels of intraspecific density dependence.

At present, it is extremely difficult to say whether any of these predictions hold in real systems, because community ecologists tend to focus on the mechanisms and strengths of interspecific interactions (Paine 1980, 1992; Laska and Wootton 1998; Wootton 2005) and largely ignore the causes and strengths of intraspecific density dependence relative to interspecific effects. Numerous interspecific interactions can generate negative intraspecific density dependence (e.g., pathogens, diseases, and parasitoids [Janzen 1970; Connell 1971; Grover 1994; Terborgh 2012], predator switching, and learning [Lawton et al. 1974; Murdoch and Oaten 1975]), but their effects would be best modeled by including these species and their mechanisms of interaction explicitly. The motivation for the analyses presented here is the myriad interactions among conspecifics that also generate negative intraspecific density dependence (Tanner 1966). For example, mortality due to cannibalism (Fox 1975; Polis 1981; Van Buskirk and Smith 1991; Rudolf 2007), opportunity costs due to time wasted in aggression, and physiological stress responses generated by interactions among conspecifics (Marra et al. 1995; Lochmiller 1996; McPeck et al. 2001a; McPeck 2004) can all reduce demographic rates as intraspecific densities increase. Territoriality and despotic habitat filling coupled to spatial variation in demographic

performance (e.g., seed germination or insect oviposition across microenvironmental gradients, variation in territory quality among nesting birds) also generate negative intraspecific density dependence (Pulliam and Danielson 1991; McPeck et al. 2001b; Both and Visser 2003; López-Sepulcre and Kokko 2005). Mate finding, mate access, and mate harassment can all also generate negative intraspecific density dependence (Bauer et al. 2005; M'Gonigle et al. 2012).

Given the importance of intraspecific density dependence to influencing the number of coexisting species in a community module (McPeck 2012 and this analysis) and to community ecological theory in general (e.g., MacArthur 1970, 1972; May 1974; Yodzis 1981; Pimm 1982; Tilman 1982; Chesson 2000; Adler et al. 2007), greater emphasis must be placed on exploring its mechanisms and consequences relative to interspecific interactions in mechanistic models of species interactions and testing the predictions of these models in real communities. Intraspecific density dependence is not simply the result of resource competition among conspecifics but rather can result from myriad processes (see previous paragraph). A very simple form of density dependence was used in this article, but future work should explore how explicit mechanisms generating intraspecific density dependence influence interspecific interactions to determine the types of species that can coexist. For example, engaging in mating interactions may increase per capita predation rates (Gwynne 1989; Sih et al. 1990; Rowe 1994), which might cause the strengths of intraspecific density dependence and predator-induced mortality rates to be positively correlated. In addition, testing these models will require experimental studies that simultaneously manipulate the causes of intraspecific density dependence and the forms and strengths of species interactions.

Holt's (1997) recognition that large communities can be dissected into a small number of community module types has also focused conceptual attention on critical structures that shape species coexistence. The analyses presented here highlight the continuity among modules, namely, a linear food chain, a guild of competing resource consumers, the diamond-shaped module, and the intraguild predation module. The various modules themselves are linked by transitions involving changes in interaction strengths and species additions (see also Krivan and Schmitz 2003). In mathematical terms, the linear food chain is the limiting condition of a simple intraguild predation module as  $\varphi \rightarrow 0$  in equation (1). Thus, Holt and Polis's (1997) criterion that the intraguild prey must be a better competitor for the basal resource than the intraguild predator is trivially true when the predator does not feed on the basal resource. Additionally, by recognizing the continuity between diamond-shaped and intraguild pre-

dation modules, we can also see that the conditions for invasibility and coexistence in these two are qualitatively identical. More generally, this approach would seem to be a rigorous and productive general framework for understanding the mechanisms of community assembly of more complex food web structures.

Incorporating the mechanisms and consequences of intraspecific density dependence into models of community modules also creates difficulties for the dominant way we have conceptualized issues of species coexistence and community structure for decades, namely, around the concept of the niche (Hutchinson 1957; MacArthur and Levins 1964; Levin 1970; MacArthur 1970, 1972; Vandermeer 1972; Chesson 1991, 2000; Leibold 1995; Adler et al. 2007; Siepielski and McPeck 2010). Intraspecific density dependence is not an additional "niche axis" in our typical metaphor for the niche. A species is not able to invade and coexist in a community because it experiences intraspecific density dependence. Rather, a species may be able to invade and coexist because other species in the system limit their own abundances and thus do not depress resources or inflate predator abundances to levels beyond which other species can invade. A shift in emphasis to Levin's (1970) limiting-factors perspective seems more productive. As Levin (1970) stated, "no stable equilibrium is possible if some  $r$  species are limited by less than  $r$  factors" (p. 418). From this perspective, the mechanisms generating intraspecific density dependence within species are simply additional potential limiting factors that promote coexistence. Many limiting factors may impinge on each species in a community, with mechanisms generating intraspecific density dependence being a possibility for each species. However, even here, the mere presence of an adequate number of limiting factors is insufficient. Understanding what mechanisms, both intraspecific and interspecific, contribute to restraining population growth rates and how these mechanisms combine to shape the demographics of interacting species is the key to understanding species coexistence and community structure.

#### Acknowledgments

I thank P. L. Chesson, R. D. Holt, T. E. Miller, R. T. Paine, and A. M. Siepielski for illuminating discussions of issues related to this article, and Chesson, J. Grover, C. Lee, Miller, Paine, Siepielski, and two anonymous reviewers for comments on drafts of the manuscript that tremendously sharpened my thinking on these issues. This work was supported by National Science Foundation grant DEB-0714782.

## Literature Cited

- Adler, P. B., J. Hille Ris Lambers, and J. M. Levine. 2007. A niche for neutrality. *Ecology Letters* 10:95–104.
- Amarasekare, P. 2008. Coexistence of intraguild predators and prey in resource-rich environments. *Ecology* 89:2786–2797.
- Arim, M., and P. A. Marquet. 2004. Intraguild predation: a widespread interaction related to species biology. *Ecology Letters* 7: 557–564.
- Armstrong, R. A., and R. McGehee. 1980. Competitive exclusion. *American Naturalist* 115:151–170.
- Bauer, S., J. Samietz, and U. Berger. 2005. Sexual harassment in heterogeneous landscapes can mediate population regulation in a grasshopper. *Ecology* 16:239–246.
- Both, C., and M. E. Visser. 2003. Density dependence, territoriality, and divisibility of resources: from optimality models to population processes. *American Naturalist* 161:326–336.
- Caswell, H., and M. G. Neubert. 1998. Chaos and closure terms in plankton food chain models. *Journal of Plankton Research* 20: 1837–1845.
- Chesson, P. L. 1991. A need for niches? *Trends in Ecology and Evolution* 6:26–28.
- . 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31:343–366.
- Chesson, P., and N. Huntly. 1997. The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *American Naturalist* 150:519–553.
- Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–310 in P. J. den Boer and G. R. Gradwell, eds. *Dynamics of populations*. Centre for Agricultural Publications and Documentation, Wageningen, Netherlands.
- Diehl, S. 1995. Direct and indirect effects of omnivory in a littoral lake community. *Ecology* 76:1727–1740.
- Diehl, S., and M. Feiße. 2000. Effects of enrichment on three-level food chains with omnivory. *American Naturalist* 155:200–218.
- Duggins, D. O. 1980. Kelp beds and sea otters: an experimental approach. *Ecology* 61:447–453.
- Estes, J. E., N. S. Smith, and J. F. Palmisano. 1978. Sea otter predation and community organization in the western Aleutian Islands, Alaska. *Ecology* 59:822–833.
- Fox, L. R. 1975. Cannibalism in natural populations. *Annual Review of Ecology and Systematics* 6:87–106.
- Gatto, M. 1991. Some remarks on models of plankton densities in lakes. *American Naturalist* 137:264–267.
- Gilpin, M. E. 1975. *Group selection in predator-prey communities*. Princeton University Press, Princeton, NJ.
- Grover, J. P. 1994. Assembly rules for communities of nutrient-limited plants and specialist herbivores. *American Naturalist* 143:258–282.
- Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. *Biological Reviews* 52:107–145.
- Gwynne, D. T. 1989. Does copulation increase the risk of predation? *Trends in Ecology and Evolution* 4:54–56.
- Harper, J. L. 1969. The role of predation is vegetational diversity. *Brookhaven Symposium of Biology* 22:48–62.
- Holt, R. D. 1997. Community modules. Pages 333–339 in A. C. Gange and V. K. Brown, eds. *Multi-trophic interactions in terrestrial ecosystems*. Blackwell, London.
- Holt, R. D., J. Grover, and D. Tilman. 1994. Simple rules for inter-specific dominance in systems with exploitation and apparent competition. *American Naturalist* 144:741–771.
- Holt, R. D., and G. A. Polis. 1997. A theoretical framework for intraguild predation. *American Naturalist* 149:745–764.
- Hutchinson, G. E. 1957. Concluding remarks. *Cold Spring Harbor Symposium of Quantitative Biology* 22:415–427.
- . 1961. The paradox of the plankton. *American Naturalist* 95: 137–145.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *American Naturalist* 104:501–528.
- Křivan, V., and S. Diehl. 2005. Adaptive omnivory and species coexistence in tri-trophic food webs. *Theoretical Population Biology* 67:85–99.
- Křivan, V., and O. J. Schmitz. 2003. Adaptive foraging and flexible food web topology. *Evolutionary Ecology Research* 5:1–30.
- Laska, M. S., and T. J. Wootton. 1998. Theoretical concepts and empirical approaches to measuring interaction strength. *Ecology* 79:461–476.
- Lawton, J. H., J. R. Beddington, and R. Bonser. 1974. Switching in invertebrate predators. Pages 141–158 in M. B. Usher and M. H. Williamson, eds. *Ecological stability*. Chapman & Hall, London.
- Leibold, M. A. 1995. The niche concept revisited: mechanistic models and community context. *Ecology* 76:1371–1382.
- . 1996. A graphical model of keystone predators in food webs: trophic regulation of abundance, incidence, and diversity patterns in communities. *American Naturalist* 147:784–812.
- Levin, S. A. 1970. Community equilibria and stability, and an extension of the competitive exclusion principle. *American Naturalist* 104:413–423.
- Lochmiller, R. L. 1996. Immunocompetence and animal population regulation. *Oikos* 76:594–602.
- López-Sepulcre, A., and H. Kokko. 2005. Territorial defense, territory size, and population regulation. *American Naturalist* 166:317–329.
- MacArthur, R. 1970. Species packing and competitive equilibrium for many species. *Theoretical Population Biology* 1:1–11.
- MacArthur, R. H. 1972. *Geographical ecology*. Princeton University Press, Princeton, NJ.
- MacArthur, R. H., and R. Levins. 1964. Competition, habitat selection, and character displacement in a patchy environment. *Proceedings of the National Academy of Sciences of the USA* 51:1207–1210.
- Marra, P. P., K. Lampe, and B. Tedford. 1995. An analysis of daily corticosterone profiles in two species of *Zonotrichia* under captive and natural conditions. *Wilson Bulletin* 107:296–304.
- May, R. M. 1974. *Stability and complexity in model ecosystems*. Princeton University Press, Princeton, NJ.
- McCann, K. S. 2012. *Food webs*. Princeton University Press, Princeton, NJ.
- McPeck, M. A. 1996. Trade-offs, food web structure, and the coexistence of habitat specialists and generalists. *American Naturalist* 148(suppl.):S124–S138.
- . 1998. The consequences of changing the top predator in a food web: a comparative experimental approach. *Ecological Monographs* 68:1–23.
- . 2004. The growth/predation-risk trade-off: so what is the mechanism? *American Naturalist* 163:E88–E111.
- . 2012. Intraspecific density dependence and a guild of consumers coexisting on one resource. *Ecology* 93:2728–2735.
- McPeck, M. A., M. Grace, and J. M. L. Richardson. 2001a. Physio-

- logical and behavioral responses to predators shape the growth/predation risk trade-off in damselflies. *Ecology* 82:1535–1545.
- McPeck, M. A., N. L. Rodenhouse, R. T. Holmes, and T. W. Sherry. 2001*b*. A general model of site-dependent population regulation: population-level regulation without individual-level interactions. *Oikos* 94:417–424.
- Menge, B. A. 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs* 65: 21–74.
- M'Gonigle, L. K., R. Mazzucco, S. P. Otto, and U. Dieckmann. 2012. Sexual selection enables long-term coexistence despite ecological equivalence. *Nature* 484:506–509.
- Murdoch, W. W., and A. Oaten. 1975. Predation and population stability. *Advances in Ecological Research* 9:1–131.
- Mylius, S. D., K. Klumpers, A. M. de Roos, and L. Persson. 2001. Impact of intraguild predation and stage structure on simple communities along a productivity gradient. *American Naturalist* 158: 259–276.
- Neubert, M. G., T. Klanjscek, and H. Caswell. 2004. Reactivity and transient dynamics of predator-prey and food web models. *Ecological Modeling* 179:29–38.
- Paine, R. T. 1966. Food web complexity and species diversity. *American Naturalist* 100:65–75.
- . 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia (Berlin)* 15:93–120.
- . 1980. Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* 49:666–685.
- . 1992. Food web analysis through field measurement of per capita interaction strength. *Nature* 355:73–75.
- Paine, R. T., and R. L. Vadas. 1969. The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. *Limnology and Oceanography* 14:710–719.
- Pimm, S. L. 1982. *Food webs*. Chapman & Hall, London.
- Pimm, S. L., and J. H. Lawton. 1978. On feeding on more than one trophic level. *Nature* 275:542–544.
- Polis, G. A. 1981. The evolution and dynamics of intraspecific predation. *Annual Review of Ecology and Systematics* 12:225–251.
- Polis, G. A., C. A. Myers, and R. D. Holt. 1989. The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual Review of Ecology and Systematics* 20:297–330.
- Polis, G. A., and D. R. Strong. 1996. Food web complexity and community dynamics. *American Naturalist* 147:813–846.
- Pulliam, H. R., and B. J. Danielson. 1991. Sources, sinks, and habitat selection: a landscape perspective on population dynamics. *American Naturalist* 137(suppl.):S50–S66.
- Revilla, T. 2002. Effects of intraguild predation on resource competition. *Journal of Theoretical Biology* 214:49–62.
- Rowe, L. 1994. The costs of mating and mate choice in water striders. *Animal Behaviour* 48:1049–1056.
- Rudolf, V. H. W. 2007. The interaction of cannibalism and omnivory: consequences for community dynamics. *Ecology* 88:2697–2705.
- Schellenkens, T., and T. van Kooten. 2012. Coexistence of two stage-structured intraguild predators. *Journal of Theoretical Biology* 308: 36–44.
- Siepielski, A. M., and M. A. McPeck. 2010. On the evidence for species coexistence: a critique of the coexistence program. *Ecology* 91:3153–3164.
- Sih, A., J. Krupa, and S. Travers. 1990. An experimental study on the effects of predation risk and feeding regime on the mating behavior of the water strider. *American Naturalist* 135:284–290.
- Tanabe, K., and T. Namba. 2005. Omnivory creates chaos in simple food web models. *Ecology* 86:3411–3414.
- Tanner, J. T. 1966. Effects of population density on growth rates of animal populations. *Ecology* 47:733–745.
- Terborgh, J. 2012. Enemies maintain hyperdiverse tropical forests. *American Naturalist* 179:303–314.
- Tilman, D. 1982. *Resource competition and community structure*. Princeton University Press, Princeton, NJ.
- . 1987. The importance of the mechanisms of interspecific competition. *American Naturalist* 129:769–774.
- Van Buskirk, J., and D. C. Smith. 1991. Density-dependent population regulation in a salamander. *Ecology* 72:1747–1756.
- Vance, R. 1978. Predation and resource partitioning in one predator–two prey model communities. *American Naturalist* 112:797–813.
- Vandermeer, J. H. 1972. Niche theory. *Annual Reviews of Ecology and Systematics* 3:107–132.
- Volterra, V. 1928. Variations and fluctuations of the number of individuals in animal species living together. *Journal du Conseil Permanent International pour l'Exploration de la Mer* 3:3–41.
- Winemiller, K. O. 1990. Spatial and temporal variation in tropical fish trophic networks. *Ecological Monographs* 60:331–367.
- Woodward, G., and A. G. Hildrew. 2002. Body-size determinants of niche overlap and intraguild predation within a complex food web. *Journal of Animal Ecology* 71:1063–1074.
- Wootton, T. J. 2005. Field parameterization and experimental test of the neutral theory of biodiversity. *Nature* 433:309–312.
- Yodzis, P. 1981. The stability of real ecosystems. *Nature* 289:674–676.

Associate Editor: Oswald J. Schmitz  
 Editor: Judith L. Bronstein