Intraspecific density dependence and a guild of consumers coexisting on one resource

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Abstract. The importance of negative intraspecific density dependence to promoting species coexistence in a community is well accepted. However, such mechanisms are typically omitted from more explicit models of community dynamics. Here I analyze a variation of the Rosenzweig-MacArthur consumer–resource model that includes negative intraspecific density dependence for consumers to explore its effect on the coexistence of multiple consumers feeding on a single resource. This analysis demonstrates that a guild of multiple consumers can easily coexist on a single resource if each limits its own abundance to some degree, and stronger intraspecific density dependence permits a wider variety of consumers to coexist. The mechanism permitting multiple consumers to coexist works in a fashion similar to apparent competition or to each consumer having its own specialized predator. These results argue for a more explicit emphasis on how negative intraspecific density dependence is generated and how these mechanisms combine with species interactions to shape overall community structure.

Key words: coexistence; guild; intraspecific density dependence; resource competition; Rosenzweig-MacArthur consumer–resource model; species richness.

Introduction

A central tenet of community ecology is that more than one consumer cannot coexist on a single resource without external constraints that limit the consumers' abundances. With only one resource present, the consumer that can depress the resource's abundance to the lowest level should monopolize that resource because no other consumer can support a population at that resource level (Volterra 1928, MacArthur and Levins 1964, Levins 1968, Tilman 1982): this is the R^* rule (Tilman 1982). For multiple consumers to coexist, either multiple resources must be present (e.g., MacArthur 1970, Tilman 1982), or some external mechanism must prevent resource monopolization by any one consumer. For example, a predator may depress the abundances of consumers below levels that prevent competitive exclusion (Paine 1966). However, models of keystone predation suggest that a single predator added to a community with only one basal resource will permit at most two consumers in the community: one consumer specialized on utilizing the resource and the other specialized on defending against the predator (Levin 1970, Holt et al. 1994, Leibold 1996, McPeek 1996). For predators to favor many consumers on a single basal resource, each consumer must have its own specialized predator (Grover 1994). Other mechanisms besides predation have also been suggested to prevent resource monopolization, including disturbance (Connell 1978, Sousa 1979, Chesson and Huntly 1997) and temporal variability (Levins 1968, Armstrong and McGehee 1980, Chesson and Warner 1981, Chesson 1985, Huisman and Weissing 1999, Gravel et al. 2011). However, most require particular conditions to foster coexistence instead of simply slowing the rate of species loss from a community (Chesson and Huntly 1997).

Another central tenet of community ecology is that coexistence requires species to have stronger effects on regulating their own abundances than they have on the regulation of other species' abundances (MacArthur 1972, Tilman 1982, Chesson and Huntly 1997, Chesson 2000, Adler et al. 2007, Chesson and Kuang 2008, Siepielski and McPeek 2010). This implies that mechanisms generating and modulating the strength of negative intraspecific density and frequency dependence fundamentally influence the structure of communities. Numerous observational and experimental studies have suggested the importance of intraspecific density and frequency dependence for coexistence in species-rich communities, including studies of forest trees (e.g., Clark and McLachlan 2003, Levine and HilleRisLambers 2009, Comita et al. 2010, Mangan et al. 2010, Kobe and Vriesendrop 2011, Terborgh 2012), annual plants (e.g., Harpole and Suding 2007), and insects in lakes (e.g., McPeek 1998, Siepielski et al. 2011). Interactions with other species can generate negative intraspecific density and frequency dependence (e.g., the Janzen-Connell hypothesis [Janzen 1970, Connell 1971, Terborgh 2012], prey switching or learning by predators [Lawton et al. 1974, Murdoch and Oaten 1975]), but innumerable mechanisms resulting from interactions among conspecifics can also generate these demographic effects (e.g., aggression and interference [Van Buskirk

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and Smith 1991], physiological stress [Lochmiller 1996, McPeek et al. 2001b], territoriality [Both and Visser 2003, López-Sepulcre and Kokko 2005], spatial aggregation and variation [Pulliam and Danielson 1991, McPeek et al. 2001a], interactions over mates [Bauer et al. 2005]).

Our understanding of the importance of negative intraspecific density and frequency dependence for coexistence is based largely on results from phenomenological models, such as Lotka-Volterra competition, where the relative strengths of intraspecific and interspecific effects among species are simply specified as parameters (e.g., MacArthur 1970, May 1974, Chesson 2000, Adler et al. 2007, Yenni et al. 2012). Moreover, our understanding that the number of consumers is limited by the number of available resource types is based on models that largely omit negative intraspecific density and frequency dependence in the consumers (e.g., Levin 1970, MacArthur 1970, Pimm 1982, Tilman 1982). In this paper I combine these two central tenets of community ecology to explore whether multiple consumers can coexist on a single shared resource if each consumer experiences some degree of negative intraspecific density dependence. I use a variation of a classic consumer–resource model and show that indeed multiple consumers can coexist on a single resource, and that the opportunity for a greater variety of coexisting consumers increases with the strength of negative intraspecific density dependence.

Model and analyses

In this analysis, I use a modified version of the Rosenzweig-MacArthur (1963; Rosenzweig 1969) consumer–resource model as a basic framework. Here, multiple consumers (N_i) feed on one resource (R), but each consumer can experience some degree of negative intraspecific density dependence in its per capita death rate. The full model is

$$\frac{dR}{dt} = R\left(c - dR - \sum_{i=1}^{n} \frac{a_i N_i}{1 + a_i h_i R} \right)$$

$$\frac{dN_i}{dt} = N_i \left(\frac{b_i a_i R}{1 + a_i h_i R} - (f_i + g_i N_i) \right). \qquad (1)$$

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). For the n consumers, each feeds on the resource according to Holling's (1959) disc equation. For consumer species i, a_i defines the attack coefficient, h_i the handling time, and b_i the efficiency of converting resources 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). Variations of this model have been used to explore patterns of population dynamics (e.g., Gilpin 1975, Gatto 1991, Caswell and Neubert 1998, Neubert et al. 2004), but not coexistence of multiple consumers. In this model, the only interactions among the consumers occur indirectly through their feeding on the shared resource.

No intraspecific density dependence

First consider the outcome of resource competition among multiple consumers when each consumer's per capita death rate does not change with its own abundance (i.e., all $g_i = 0$). The basic intuition about the outcome is easiest to develop when all species have a linear functional response (i.e., all $h_i = 0$) and only two consumers are initially present. The isoclines for two consumers and the resource in this case are illustrated in Fig. 1A. The isocline for the resource is a plane that crosses the R-axis at c/d (which is the equilibrium abundance of the resource in the absence of all consumers) and that crosses each consumer's axis at c/a_i. The isocline of each consumer is also a plane, and each crosses the R-axis at $R^*_{(i)} = f_i/(a_i b_i)$. This is also the equilibrium resource abundance in a community with only consumer i and the resource present (signified by the parenthetical i subscript). Each consumer's abundance will increase if $R > f_i/(a_i b_i)$ and will decrease if $R < f_i/(a_i b_i)$. However, each consumer isocline is parallel to all consumer axes, and so the consumer isoclines are all mutually parallel; in other words, the consumer isoclines never intersect (Fig. 1A). Here, coexistence of multiple consumers on the single shared resource is impossible because of the geometry of the isoclines. This is another representation of the R^* rule (Tilman 1982). In this case, the consumer with the isocline crossing the R axis at the lowest value (i.e., lowest $R^*_{(i)} = f_i/a_i b_i$) can drive the resource abundance low enough that all other consumers will become extinct: this consumer has the lowest R^* and is the superior competitor in this case.

The same result holds with a saturating functional response (i.e., $h_i > 0$). In this case, the consumer isoclines are still planes that are parallel to all consumer axes and so to one another, and thus do not intersect. Each consumer isocline now crosses the R axis at $R^*_{(i)} = [f_i/a_i(b_i - f_i h_i)]$: the consumer with the lowest value for this quantity will drive all others extinct by depressing the resource abundance to levels at which no other consumer can exist.

Intraspecific density dependence

When consumers experience some degree of intraspecific density dependence (i.e., $g_i > 0$), the geometry of the system changes to allow multiple consumers to
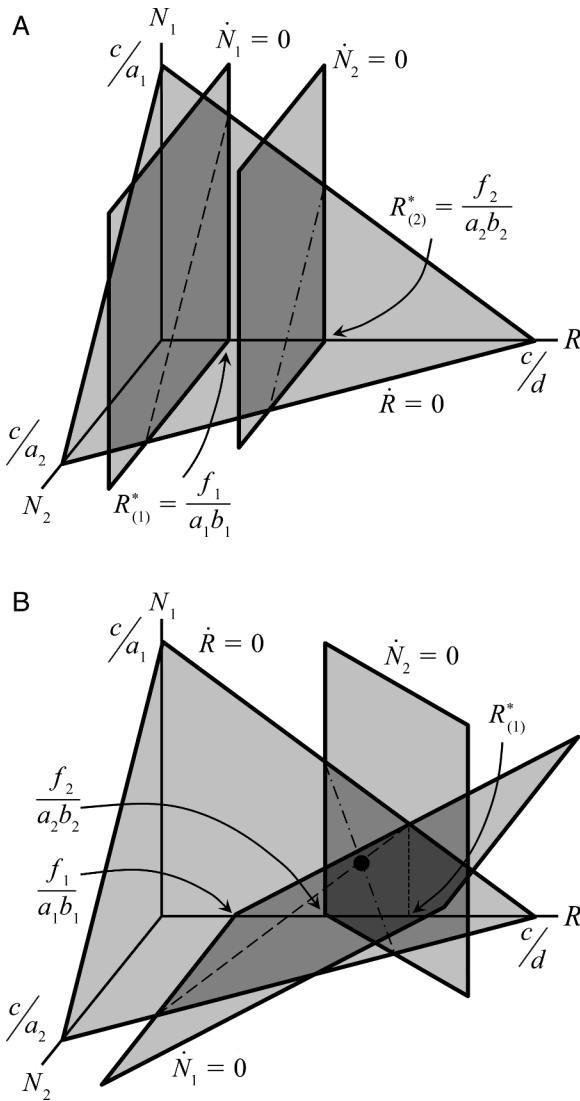
FIG. 1. Isocline systems resulting from various parameter assumptions with two consumers (N_1 and N_2) feeding on one resource (R). (A) The three-dimensional system of isoclines when the consumers have linear functional responses (i.e., $h_1 = h_2 = 0$), and neither consumer experiences any intraspecific density dependence (i.e., $g_1 = g_2 = 0$). (B) A comparable three-dimensional system of isoclines when the two consumers experience intraspecific density dependence (i.e., $g_1 > 0$ and $g_2 > 0$). In both panels, the isocline for the resource is labeled $\dot{R} = 0$, the isocline for consumer 1 is labeled $\dot{N}_1 = 0$, and the isocline for consumer 2 is labeled $\dot{N}_2 = 0$. The dashed line and the dot-dashed lines identify the lines of intersection between the resource and the consumer isoclines for N_1 and N_2, respectively. As in the text, c is the growth rate of the resource when rare, and d is the strength of density dependence in the resource; a_i is the attack rate and b_i is the conversion efficiency of consumer i on the resource; f_i is the death rate of consume i when rare. $R^*_{(i)}$ is the equilibrium abundance of the resource when only consumer i is present in the system.

coexist on one resource (Fig. 1B). With linear functional responses (i.e., $h_i = 0$), the consumer isocline still crosses the R axis at $f_i/(a_ib_i)$. However, the consumer isocline now has a positive (not infinite) slope of $(a_ib_i)/g_i$ in the N_i–R plane, but it remains independent of all other consumer abundances (Fig. 1B). When only one consumer and the resource are present, their equilibrium abundances are given by

$$R^*_{(i)} = \frac{cg_i + a_if_i}{a_i^2b_i + dg_i} \qquad N^*_{(i)} = \frac{a_ib_ic - df_i}{a_i^2b_i + dg_i} \qquad (2)$$

again where the parenthetical subscripts for R^* and N^* identify this as the equilibrium with only the resource and consumer i present. The equilibrium is feasible if $f_i/(a_ib_i) < c/d$ and always stable if it exists and no other consumers can invade (Appendix). Greater values for the strength of intraspecific density dependence (i.e., increasing g_i) do not change the intercept of consumer i's isocline on the R-axis. However, stronger intraspecific density dependence in the consumer decreases the slope of the consumer's isocline (i.e., a_ib_i/g_i), thus increasing $R^*_{(i)}$ and decreasing $N^*_{(i)}$.

Because $f_i/(a_ib_i) < R^*_{(i)}$ with negative intraspecific density dependence, other species can now invade this system and coexist with consumer i. As a convention, I number consumers in order of increasing values of $f_i/(a_ib_i)$, so that

$$\frac{f_1}{a_1b_1} < \frac{f_2}{a_2b_2} < ... < \frac{f_i}{a_ib_i} < ... < \frac{f_n}{a_nb_n}. \qquad (3)$$

Analogous to apparent competition (Holt 1977), the ordering of species by this critical ratio defines whether each species can be present in the community. The species with the lowest $f_i/(a_ib_i)$ (i.e., consumer 1 by the naming convention) will always be present if it can invade and if $[R^*_{(1)}, N^*_{(1)}]$ is a feasible equilibrium. By setting the points $f_i/(a_ib_i)$ and $R^*_{(1)}$ along the R-axis, this species also defines the range of other species that can potentially coexist (Fig. 2). To build intuition, consider the system in which consumer 1 and the resource are at their stable equilibrium (i.e., the point $[R^*_{(1)}, N^*_{(1)}, N_2 = 0]$ in Fig. 1B where the consumer 1 and resource isoclines cross in the N_1–R face). Any species with $f_i/(a_ib_i) < R^*_1$ can invade this two-species system and coexist with consumer 1, because it will have a positive population growth rate at $R^*_{(1)}$ when it is rare (Fig. 1B). Moreover, stronger intraspecific density dependence in consumer 1, which will increase $R^*_{(1)}$, will permit consumers with higher values of $f_i/(a_ib_i)$ to invade.

The isoclines for consumer 1 and the resource intersect along a line segment in three dimensions going from the two-species equilibrium $[R^*_{(1)}, N^*_{(1)}, N_2 = 0]$ in the N_1–R face to the point in the N_2–R face where

$$\left[R = \frac{f_1}{a_1b_1}, N_1 = 0, N_2 = \frac{a_1b_1c - df_1}{a_1a_2b_1} \right]$$

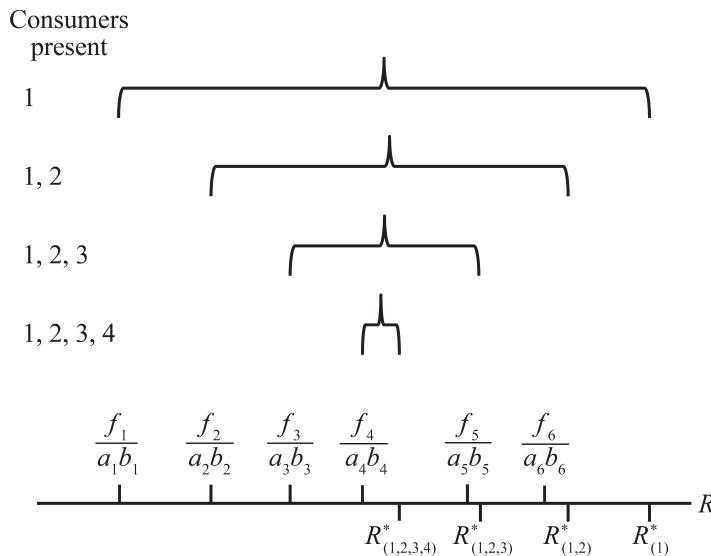(the dashed line in Fig. 1B). The isocline of any invading

FIG. 2. An illustration focusing on the resource axis from Fig. 1 to show how adding additional species causes the window of critical ratios to become smaller as more consumers invade the system. With only consumer 1 (the species that can maintain a positive population growth rate at the lowest resource abundance) in the system, any species with $f_1/(a_1b_1) < f_i/(a_ib_i) < R^*_{(1)}$ can invade the system and coexist with consumer 1; with both consumer 1 and 2 (the two species that can maintain positive population growth rates at the lowest resource abundances) in the system, any species with $f_2/(a_2b_2) < f_i/(a_ib_i) < R^*_{(1,2)}$ can invade and coexist with them; and so on. In this specific case, consumers 1–4 could coexist with one another, but consumers 5 and 6 would be excluded. Note that consumer 5 could coexist in a community that contained consumers 1, 2, and 3 but lacked consumer 4, and that consumer 6 could coexist in a community that contained consumers 1 and 2 but lacked consumers 3 and 4.

consumer must be able to intersect this line segment for the second consumer to coexist with consumer 1, and this is only possible if $f_i/(a_ib_i) < R^*_{(1)}$. This is true for consumer 2 as illustrated in Fig. 1B, and the two consumers and the resource will coexist at the point where the three planes intersect (the solid circle in Fig. 1B is a stable equilibrium if only consumers 1 and 2 can invade; see Appendix). At this new equilibrium, the abundances of the resource (identified as $R^*_{(1,2)}$) and consumer 1 have decreased as compared to their values before consumer 2 invaded.

With consumers 1 and 2 present, the criterion for the third species to invade has now become more stringent. Any new invader must now have $f_i/(a_ib_i) < R^*_{(1,2)}$; the window of possible values for the critical ratio have narrowed (Fig. 2). Imagine that consumer 3 has $f_3/(a_3b_3) < R^*_{(1,2)}$ and so can invade. This will further depress resources to $R^*_{(1,2,3)}$, and thus further constrain the possibilities for other consumers to invade (Fig. 2). Consumers can continue to invade until no absent consumers can satisfy $f_i/(a_ib_i) < R^*_{(1,2,...,j)}$ with $j < i$. Although I have illustrated this with sequential invasions, invasion order has no influence on the final composition of coexisting consumers; if all species eventually invade the community, the same set of consumers will coexist at the same equilibrium no matter the order of invasion. Also, numerical simulations indicate that all multi-consumer communities quickly arrive at their stable equilibria (Appendix).

The strengths of intraspecific density dependence among the various consumers will influence the number of species that can coexist. Remember that stronger intraspecific density dependence means that the slope of the consumer isocline decreases in the N_i–R plane, and so the consumer will depress the resource to a lesser degree. Thus, with greater intraspecific density dependence, the invasion window for subsequent species narrows more slowly with each new species added to the community, and so more species should be able to coexist.

Qualitatively identical results are obtained if the consumers have saturating functional responses (i.e., $h_i > 0$). A saturating functional response has three different effects on the isocline system (Fig. 3). The first is to cause the resource isocline to become hump-shaped as h_i increases, although the points where the resource isocline intersects the various axes do not depend on h_i (Rosenzweig and MacArthur 1963, Rosenzweig 1969). The positions and shapes of the consumer isoclines also change in two ways when consumers experience intraspecific density dependence, but the isocline for each consumer does remain independent of the other consumers' abundances, just as in the linear functional response case. As with no intraspecific density dependence, the point at which the consumer isocline crosses the R axis is given by $f_i/[a_i(b_i - h_if_i)]$, and so handling time increases the critical ratio for each species (Fig. 3). Which species can coexist will now be determined by the ordering of this slightly more complex critical ratio (and also reordering and renumbering species based on the values of the new ratios):
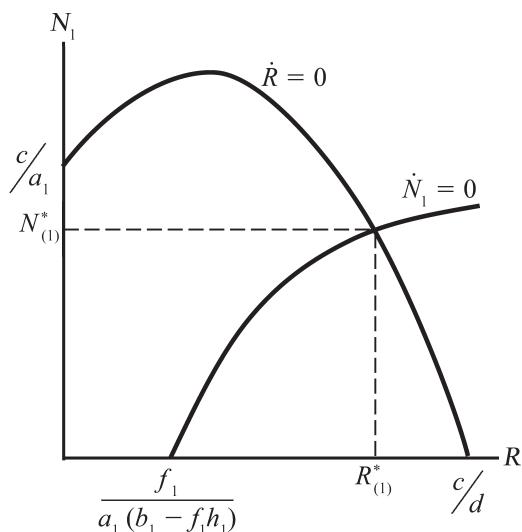
Fig. 3. The isocline system for one consumer (N_1) feeding on the resource (R), in which the consumer has a saturating functional response (i.e., $h_1 > 0$) and experiences intraspecific density dependence (i.e., $g_1 > 0$). Greater values of h_1 cause the prey isocline to bow farther up, the R intercept of the consumer isocline to slide to the right, and the asymptote of the consumer isocline to move closer to the R-axis. As a result, $R^*_{(1)}$ increases as h_1 increases.

$$\frac{f_1}{a_1(b_1 - f_1 h_1)} < \frac{f_2}{a_2(b_2 - f_2 h_2)} < ... < \frac{f_i}{a_i(b_i - f_i h_i)}$$

$$< ... < \frac{f_n}{a_n(b_n - f_n h_n)}. \qquad (4)$$

(Note that this will also accommodate any combination of species with saturating ($h_i > 0$) and linear ($h_i = 0$) functional responses together.) In addition, handling time—when combined with negative density dependence—causes the consumer isocline to bend away from its own axis (although each consumer's isocline remains independent of the other consumers' abundances) and toward the R-axis to eventually asymptote at $P_i = (b_i - f_i h_i)/(g_i h_i)$, which will increase the value of $R^*_{(i)}$ with increasing h_i (Fig. 3; see also Gatto 1991). As a result, colonizing consumers will depress resource abundance to a lesser degree because of predator satiation. The window of available critical ratios for invasion will also change as a result of predator satiation, but the fundamental dynamics of the system remain the same. Also, increasing handling times permit greater scope for more species to potentially enter the community, because $R^*_{(i)}$ increases faster than

$$\frac{f_i}{a_i(b_i - h_i f_i)}$$

with increasing h_i for large areas of parameter space. Numerical simulations of the full system indicate that across a wide range of parameter space the system converges to a stable equilibrium (Appendix). The only exceptions are limit cycles that result when the consumer

isocline crosses the resource isocline once and far to the left of the hump (see Appendix): these are essentially the same conditions that give limit cycles in the original model without consumer intraspecific density dependence and are caused by the consumer being able to overexploit the resource (Rosenzweig and MacArthur 1963, Rosenzweig 1969).

DISCUSSION

This analysis of a simple consumer–resource model has shown that negative intraspecific density dependence (and by extension frequency dependence among community members) can have profound consequences on community structure. Specifically, resource competitors are not required to be differentiated into "niches" to coexist. By adding negative intraspecific density dependence, no species can increase to an abundance at which it can completely monopolize the resource. When resource abundance is the only limit on consumer abundance, the level to which the consumer can depress the resource is also the level at which the consumer first has a positive population growth rate (Fig. 1A). Consequently, the consumer that can depress the resource to the lowest level is the only consumer that can have a positive population growth rate at that level (Tilman 1982). Negative intraspecific density dependence creates a gap between these two levels, and thus creates the opportunity for other species to exploit the resource at a level below which the best resource exploiter, defined by R^*, can depress that resource (Fig. 1B). For each species, the strength of intraspecific density dependence defines the width of this gap, with the lower end being the lowest resource level at which the population can have a positive overall population growth rate (i.e., $f_i/[a_i (b_i - h_i f_i)]$) and the upper end being the level to which the consumer can depress the resource when it is the only consumer present (i.e., $R^*_{(i)}$) (Fig. 2). Thus, the emphasis shifts from which consumer can depress resources to the lowest level in monoculture to which consumer can support a population at the lowest resource level. This also implies that multispecies assemblages of consumers should depress resource levels below what any can in monoculture, if intraspecific density dependence is important.

More importantly, this shows how many more species can coexist in a system than the number of available niche axes along which they can differentiate. The paradox of community ecology has always been that many systems contain many more species than apparent niche axes (e.g., Hutchinson 1961, Armstrong and McGehee 1980). How can so many insect species all coexist while feeding on the same host plant (e.g., Condon et al. 2008), or how can so many plant species coexist while competing for so few resources (e.g., Hutchinson 1961, Grubb 1977, Tilman 1982, Chesson 1991, Adler et al. 2007)? The recognition that intraspecific density dependence limits a species' ability to

completely monopolize a given resource shows how each niche axis can support a guild of species (Root 1967), without guild members being differentiated in any substantial way or having more subtle trade-offs that further subdivide niche space. Each guild member must simply limit its own abundance to some degree, which leaves resources available to be utilized by other guild members. More guild members should also be able to coexist on a single resource with greater levels of negative intraspecific density dependence, because the available range of potential resources that additional consumers can exploit is increased (Fig. 2).

Whether one considers intraspecific density dependence generated by interactions among conspecifics to be an additional "niche axis" for a species is a semantic issue that may confuse more than clarify. Intraspecific density dependence in one species does not permit that species into the system; rather by limiting its own abundance it permits another species into the system. In this case, Hutchinson's (1957) heuristic metaphor of niches and niche axes may not be a useful representation for understanding this mechanism promoting coexistence. Intraspecific density dependence prevents the species that can support a population at the lowest resource level from completely monopolizing the resource. Additional consumer species can coexist with this species if they can support populations on what remains. Here, ecological differentiation among the consumers is not the issue. Also, if the abundance of one consumer directly affected the ecological performance of other consumers (not modeled here), fewer consumers would coexist as well. Understanding the balance of all these demographic forces propagating through the food web is needed to usefully understand the mechanisms fostering coexistence.

The mechanics for how negative intraspecific density dependence permits the coexistence of multiple species on one resource works exactly like apparent competition (Holt 1977, 1984), only in reverse. In fact, in reviewing a preliminary draft of this manuscript, R. D. Holt (*personal communication*) called these results "apparent competition in Lewis Carroll's looking glass." Apparent competition is the moniker for a community module in which multiple self-limited resources are all fed upon by a single consumer (e.g., in Eq. 1 a single N feeds upon multiple R species) (Holt 1977). The number and types of resource species that can coexist is determined by the species having the largest ratio of intrinsic growth rate to predator attack rate: using the notation of the present paper and identifying the multiple R species and their parameters by $k = 1, 2, \ldots, m$, this would be the species with the largest value for c_k/a_k (Holt 1977). When resources are ranked in descending order based on this ratio, some number of the top species in the ranking can coexist. Each resource species added to the system inflates the consumer's abundance until no other resource has a value of c_k/a_k that permits it to support a population in

the face of this shared predator (Holt 1977). Interestingly, if the resources are not self-limiting (i.e., all $d_k = 0$ in Eq. 1), only the resource with the highest c_k/a_k can coexist with the consumer because the resources' isoclines do not intersect. The symmetry of apparent competition with the mechanism described here is unmistakable (Fig. 2). This also suggests that when these two mechanisms are combined, many more than two intermediate trophic-level consumers may be able to coexist in a keystone predation community module with one basal resource and one top predator (Levin 1970, Holt et al. 1994, Leibold 1996, McPeek 1996). A formal analysis of this conjecture is currently underway (M. A. McPeek, *unpublished manuscript*).

The mechanism considered here also works in nearly identical fashion to one considered by Grover (1994), in which the abundance of each consumer is limited by a specialized predator. Grover (1994) showed that multiple consumers can coexist on a single, shared resource if each specialized predator prevents its prey (i.e., the consumer on which each feeds) from overexploiting the resource. While being inspired by Grover's (1994) investigation, my present analysis illustrates that mechanisms generated by interactions among conspecifics can achieve the same outcome without the need to invoke a specialized predator for each coexisting consumer. Many different interactions among conspecifics can generate negative density dependence. For example, mortality due to cannibalism is an obvious example that is prevalent in many animal taxa and has been shown to strongly influence community structure (Fox 1975, Polis 1981). Physiological stress responses generated by interactions among conspecifics, even if no mortality occurs, can also substantially reduce an individual's demographic performance with increasing density (Marra et al. 1995, Lochmiller 1996, McPeek et al. 2001a; see also Boonstra et al. 1998, McPeek 2004, and Hawlena and Schmitz 2010 for similar stress responses to predators). Territoriality and despotic habitat filling when coupled with spatial variation in habitat quality (e.g., seeds germinating in different microenvironments, or territory quality varying among nesting pairs of birds) can easily generate negative density dependence (Pulliam and Danielson 1991, McPeek et al. 2001b). Mate access, mate finding and mate harassment can as well promote coexistence (Bauer et al. 2005, M'Gonigle et al. 2012). These and other interactions among conspecifics can generate forms of negative intraspecific density dependence that can lead to the kind of mechanism modeled here (Tanner 1966). Moreover, the combination of specialized predators/diseases (Janzen 1970, Connell 1971, Grover 1994) and intraspecific mechanisms generating density dependence would presumably permit even more coexisting species than either could separately.

Including intraspecific density dependence for species at higher trophic levels in community models has been criticized in the past, primarily because it too easily fosters the stability of large multispecies communities in randomly assembled food webs (cf. Gardner and Ashby 1970,

Lawton and Pimm 1978, Pimm and Lawton 1978, Yodzis 1981, Pimm 1982). However, the variety and commonness of mechanisms that generate intraspecific density dependence across taxa would seem to argue for their inclusion on biological grounds (Tanner 1966, Yodzis 1981). Moreover, simple multitrophic-level models including intraspecific density dependence predict certain patterns of community response that models lacking them do not. For example, simple food chain models including intraspecific density dependence at higher trophic levels better predict changes in overall trophic biomass across productivity gradients than models lacking it (cf. Okasanen et al. 1981, Gatto 1991, Gleeson 1994).

The concept of the niche and what that concept implies (e.g., competitive exclusion, limiting similarity, trade-offs) has dominated the way we think about species coexistence and community structure for decades (Hutchinson 1957, MacArthur and Levins 1964, Levin 1970, MacArthur 1970, 1972, Chesson 1991, 2000, Leibold 1995, Adler et al. 2007, Siepielski and McPeek 2010). Species are certainly differentiated among niches in real communities, but the present analysis shows how guilds of species can stably coexist within each niche, if intraspecific mechanisms generating density dependence also limit their abundances. In other words, intraspecific density dependence may foster multiple species occupying each available niche in a community. Thus, understanding how trade-offs cause species differentiation is necessary but insufficient to fully explain coexistence. We must also understand how mechanisms generating intraspecific density dependence—in particular those mechanisms that result from interactions among conspecifics—prevent species from monopolizing some ecological opportunity in a community. Coexistence is not just a need for niches.

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SUPPLEMENTAL MATERIAL

Appendix

Stability analyses for models presented in the main text (*Ecological Archives* E093-253-A1).