Consumer Effects on the Vital Rates of Their Resource Can Determine the Outcome of Competition between Consumers

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abstract: Current competition theory does not adequately address the fact that competitors may affect the survival, growth, and reproductive rates of their resources. Ecologically important interactions in which consumers affect resource vital rates range from parasitism and herbivory to mutualism. We present a general model of competition that explicitly includes consumer-dependent resource vital rates. We build on the classic MacArthur model of competition for multiple resources, allowing direct comparison with expectations from established concepts of resource-use overlap. Consumers share a stage-structured resource population but may use the different stages to different extents, as they do the different independent resources in the classic model. Here, however, the stages are dynamically linked via consumer-dependent vital rates. We show that consumers' effects on resource vital rates result in two important departures from classic results. First, consumers can coexist despite identical use of resource stages, provided each competitor shifts the resource stage distribution toward stages that benefit other species. Second, consumers specializing on different resource stages can compete strongly, possibly resulting in competitive exclusion despite a lack of resource stage-use overlap. Our model framework demonstrates the critical role that consumer-dependent resource vital rates can play in competitive dynamics in a wide range of biological systems.

Keywords: competition, coexistence, consumer dependence, resource-use overlap, consumer-resource models, stage structure.

Introduction

From foundational models to current ones, the ecological theory of resource competition and competitive coexistence has focused on the rates at which consumer populations deplete their shared resources through consumption (e.g., MacArthur and Levins 1967; Tilman 1982; Abrams and Rueffler 2009). These studies emphasize the role of overlap and efficiency in consumers' resource use in determining competitive coexistence or exclusion. Yet resource depletion

is only one way in which consumers affect resource abundance. Nature abounds with examples in which consumers ingest only portions of resource individuals or consume products or substances produced by resource individuals, sometimes in exchange for a service. A prominent ecological feature of these interactions is the effect of consumers on resource vital rates (survival, growth, and reproduction). We refer to effects other than direct depletion of resource biomass as nonconsumptive, although these effects frequently result from the act of consumption. Examples include the effects of pathogens and parasites and some parasitoids that do not immediately or completely consume their hosts; most herbivores, which allow their plant hosts to survive, grow, and reproduce at reduced rates; nonlethal predators; and mutualists, which may collect nectar, food bodies, or pollen from plants while pollinating or protecting them (Holland and DeAngelis 2010). In addition, lethal predators frequently affect the behavior and foraging activity of surviving prey (e.g., Preisser et al. 2007). The magnitude of these effects on resource dynamics may be unique to each consumer species (such as pathogens that vary in their degree of virulence). In most quantitative competition theory, however, the parameters determining resource supply or renewal rates are constants, prohibiting the explicit inclusion of consumer-dependent changes in resource renewal dynamics. To our knowledge, there is as yet no synthetic extension of classic competition theory to consumer effects on resource vital rates and, as a result, no general guidance for expectations of how these effects can influence competitive coexistence and exclusion.2

Keeping in mind the diversity of species interactions in which consumers affect resource vital rates, we illustrate the development of a general model using herbivory as our primary example. Herbivore-plant interactions are a major class of consumer-resource relationships, yet a comprehensive theoretical framework for competition among herbivores is still lacking (Kaplan and Denno 2007). One reason for this dearth of theory has been a long-standing contro-

versy over whether competition is an important force structuring communities of herbivores (reviewed in Denno et al. 1995; Kaplan and Denno 2007). The current consensus is that recent experimental work supports the occurrence of resource competition between herbivores, emphasizing the role of host-plant responses (including inducible defenses; e.g., Long et al. 2007; Anderson et al. 2009) in mediating these interactions (Denno et al. 1995; Kaplan and Denno 2007). Still unresolved, however, are long-standing questions regarding whether herbivore use of different plant parts, developmental stages, and even individual plants should be interpreted as evidence of competition between herbivores (e.g., Janzen 1973; Kaplan and Denno 2007) or as evidence of stabilizing resource partitioning (e.g., Haigh and Maynard Smith 1972; Daugherty 2009). A theoretical framework that integrates herbivore use of host-plant resources and host-plant responses to herbivory is needed to resolve the roles of co-occurrence and ecological similarity in competition between herbivores.

Plant survival, growth, and reproductive rates respond to herbivory and are therefore capable of mediating herbivore-herbivore interactions. Plant vital rates typically vary across size classes or life-history stages (e.g., Caswell 2001), and numerous studies document effects of herbivory on stage-specific vital rates that can be expected to alter the dynamics of the host population (e.g., Crawley 1997; Maron and Crone 2006). Several studies explicitly connect plant-consumer interactions with plant stage structure, thereby demonstrating an effect of consumers' use of resources on plant population dynamics (e.g., Knight 2004; Miller et al. 2009; Maron et al. 2010). None, however, have linked consumer-dependent plant dynamics back to the consumer community. A reciprocal approach is necessary to examine the hypothesis that plant vital rates can mediate herbivore competition.

We evaluate this hypothesis using a model framework that combines classic competition theory with consumer-dependent resource vital rates, with particular focus on stage-structured resources. Resource consumption and consumer population dynamics take place according to MacArthur's consumer-resource model (MacArthur and Levins 1967; MacArthur 1970). This influential model quantifies consumer use of multiple independent resources, with the degree of resource-use overlap being key to consumer coexistence. We modify this model so that the different resources are the nonindependent life stages of a single resource species. This enables us to apply the explanatory power of the classic theory to the broad range of species interactions described above, using the widespread, familiar, and data-friendly projection matrix approach for the resource dynamics.

Previous studies have investigated the possibility of consumer coexistence via differential use of a single resource population structured by developmental stage, size, or within-individual physiology (Haigh and Maynard Smith 1972; Briggs 1993; Wilson et al. 1999; Farnsworth et al. 2002; Murdoch et al. 2003; de Roos et al. 2008; Daugherty 2009). As in the special case of herbivory, differing results emerging from different studies have hampered generalization across these disparate biological systems. Our approach enables us to draw general conclusions about a range of resource-use scenarios and to compare them directly to well-established expectations, identifying specific contributions of resource-use overlap and consumer effects on resource vital rates to competitive exclusion and coexistence. Here we identify consumer alteration of the resource distribution through effects on resource dynamics as a key determinant of competitive outcomes; this mechanism is common to previous studies and reconciles their apparently disparate conclusions. Throughout, we relate our analysis to important and familiar extensions of MacArthur-type theory, perhaps the best known of which is the R^* concept (Tilman 1982).

In the next sections, we introduce the model and present analytic results for simplified resource dynamics. We then use simulations to elaborate on our findings under less restrictive assumptions, including a more realistic resource life history. Throughout, we present results for the two endpoints that bracket the range of resource-use possibilities for two consumer species: consumers that use resource stages identically and consumers that specialize on different resource stages.

The Model: Consumer-Resource Dynamics with Consumer-Dependent Resource Vital Rates

Our theoretical framework builds on established theory for consumers of multiple resources (MacArthur and Levins 1967; MacArthur 1970; Chesson 1990; Haygood 2002). We use the same equations and assumptions as in previous work, with two key modifications: (1) instead of independent resources, we include dynamic interactions among developmental stages of a single resource population, and (2) we allow for resource demographic rates to depend on consumer identity. To incorporate resource demography, we distinguish between consumable resources, such as phloem, leaf tissue, seeds, or nectar, and the resource individuals that produce these consumable resources. We assume that the supply of consumable resources depends on the number and age, size, or developmental stage (hereafter simply "stage") of resource individuals, so that it will be equivalent to discuss consumption of consumable resources and control or capture of resource individuals, and we track the numbers of resource individuals in each stage using a discrete-time demographic projection matrix (Caswell 2001). The elements of the resource projection matrix depend on resource use by consumers (below).

There are N species of consumers C_i ($i = 1, \ldots, N$) in the consumer community; the vector $\mathbf{C}(t)$ refers to all consumers at time t. Following MacArthur and Levins (1967), each unit of consumer species i consumes the resources produced by resource individuals in stage j at the rate u_{ij} per unit resource. In the classic model, this formulation means that the amount of resource j consumed by each consumer species per unit time ($u_{ij}C_i(t)R_j(t)$, where $R_j(t)$ denotes the abundance of resource j at time t) is linearly related to the consumers' densities. We retain this property in our discrete-time framework by introducing $\mu_{ij}(t) = f(u_{ij}, \mathbf{C}(t))$, the fraction of resource individuals of stage j in one time step that is captured or controlled by species i. This prevents the total resources consumed ($u_{ij}R_j(t)$) from exceeding the amount available in that time step ($R_j(t)$):

$$\mu_{ij}(t) = \begin{cases} u_{ij}C_i(t) & \text{if } \sum_i u_{ij}C_i(t)R_j(t) \leq R_j(t) \\ \dfrac{u_{ij}C_i(t)}{\sum_i u_{ij}C_i(t)} & \text{if } \sum_i u_{ij}C_i(t)R_j(t) > R_j(t) \end{cases}. \quad (1)$$

Thus, when resources are abundant relative to consumer demand, resource capture takes place as in the classic model; when combined consumer demand exceeds the resource supply in a given time step (which eventually limits consumer populations), each consumer species consumes a fraction of what is available, in proportion to its relative abundance in the consumer community. We do not consider nonlinear consumer functional responses here (e.g., Abrams 1980; Tilman 1982), in order to facilitate comparison with classic results and to establish a baseline for comparison with more complex models. We provide further interpretation of equation (1), including the minimum resource supply for each consumer (e.g., Tilman 1982), in the appendix in the online edition of the *American Naturalist*.

To complete the description of consumer dynamics, we again follow previous theory (MacArthur 1970; Chesson 1990; Haygood 2002) and let the constants β_{ij} be the benefit or value to consumer i of a resource individual of stage j, or, in other words, the conversion efficiency of resources into consumer units. These β_{ij} depend on the physiological conversion of a resource into consumer biomass as well as the amount of consumable resource produced by resource individuals in the jth stage. The consumer populations grow at per capita rates proportional to per capita resource consumption:

$$C_i(t+1) = \sum_j \beta_{ij} \frac{\mu_{ij}(t)R_j(t)}{C_i(t)} C_i(t) = \sum_j \mu_{ij}(t)\beta_{ij}R_j(t). \quad (2)$$

This equation expresses the dependence of consumer dynamics on patterns of resource use (via the $\mu_{ij}(t)$) as well as the dynamics of the different resource stages and their relative benefits (via the $\beta_{ij}R_j(t)$).

To describe the dynamics of the structured resource population, we let the vector $\mathbf{R}(t)$ contain the abundance of all resource stages at time t. The dynamics of the resource population are determined by the consumer-dependent projection matrix $\mathbf{M}(\mathbf{C}(t))$, which describes resource transitions among stages—stasis, growth or shrinkage, and fecundity, all conditioned on survival—as functions of consumer densities. To limit total population abundance and, in the case of mutalism, to prevent runaway positive feedbacks, we introduce additional resource density dependence. Because the purpose of density dependence here is only to ensure that population sizes remain finite, we apply the same density effects to all resource stages. Although not intended to be realistic, this is a useful starting point because it does not alter the relative abundance of resource stages and so does not directly affect competition between consumers (e.g., Lee and Inouye 2010); a simple model helps uncover the mechanisms by which consumer-dependent resource dynamics alter competitive dynamics. Given these assumptions, the functional form of density dependence in the resource is not important. We choose a Ricker function,

$$\mathbf{R}(t+1) = \mathbf{M}(\mathbf{C}(t))\mathbf{R}(t)\exp\left(-b\sum_j R_j(t)\right), \quad (3)$$

which is convenient because it permits consumers to affect both resource growth rate and equilibrium abundance through the transition matrix $\mathbf{M}(\mathbf{C}(t))$. The parameter b controls the strength of density dependence, which we assume is a function of total population size. We discuss the implications of density dependence in more detail in the appendix.

The kjth element of $\mathbf{M}(\mathbf{C}(t))$ is equal to the sum over all consumers of its value when used by consumer i, m'_{ikj}, weighted by the probability of use by each consumer species (μ_{ij}):

$$m_{kj}(t) = \left[1 - \sum_i \mu_{ij}(t)\right]m_{kj}^0 + \sum_i \mu_{ij}(t)m'_{ikj}, \quad (4)$$

where the bracketed term is the fraction of resources of stage j that are unused, and m_{kj}^0 is the matrix element for the resource when it is unused. Thus, consumer species both affect (eqq. [3], [4]) and are affected by (eq. [2]) resource stage structure, enabling interactions among consumers beyond resource depletion by consumption. We do not specify the m'_{ikj} relative to the m_{kj}^0 because we assume that at equilibrium all resources are subject to use (but see the appendix). Thus, the signs of consumer effects (beneficial or detrimental) on the resource are also unspecified, so our results hold whether consumers are mutalists or enemies of the resource.

Analytical Coexistence Results

For simplicity, in what follows we assume two consumer species and one or two resource stages. The different stages of our single resource population may be ordered along a linear axis, such as size, but with only two resource types, this assumption is not necessary. We classify the coexistence of competitors on the basis of steady state relative consumer abundance: species coexist if they have finite, nonzero equilibrium relative population sizes. This measure of coexistence is robust to complex dynamics that could arise from Ricker density dependence (Lee and Inouye 2010; appendix).

In the absence of both resource structure and consumer effects on resource vital rates, we can easily show that two consumers coexist at equilibrium only if $\beta_1 u_1 = \beta_2 u_2$ (details given in the appendix). A competitor that consumes less of the resource (lower u_i) can compensate by converting resources into its own biomass more efficiently (greater β_i), but stable coexistence of the competitors is impossible: at best, the two can be precisely matched in performance and thus competitively equivalent, resulting in neutral dynamics. If the two are not competitively equivalent, the consumer species with higher βu (i.e., the species that can tolerate a lower resource supply rate; appendix) excludes the other (e.g., Tilman 1982). These results are independent of the equilibrium abundance of the resource, and thus any effects of either consumer on the vital rates of a single unstructured resource have no effect on competitive coexistence.

When the resource species has two stages (e.g., adult and juvenile) but its demography is unaffected by consumers, competitive coexistence of consumers can occur due to familiar mechanisms involving multiple independent resources. The resource stages equilibrate at relative abundances determined by intrinsic resource dynamics; letting A be the ratio of adults to juveniles at equilibrium (the resource supply ratio of consumable resources; e.g., Tilman 1982), we can solve for the relative equilibrium abundance of the two consumers. Stable coexistence occurs when this relative equilibrium abundance is finite and positive, which requires that

$$\frac{u_{1A}}{u_{1J}} > A\frac{\beta_{2A}u_{2A} - \beta_{1A}u_{1A}}{\beta_{1J}u_{1J} - \beta_{2J}u_{2J}} > \frac{u_{2A}}{u_{2J}} \tag{5}$$

or the same expression with both inequalities reversed (see the appendix for the derivation). As described in the appendix, this is equivalent to two independent resource types or to the case in which consumer species affect resource transition rates identically.

Equation (5) expresses two criteria that together constitute resource partitioning. First, stable coexistence cannot occur if the consumers' two resource-use functions are equal (or proportional) because this would result in equality of the right and the left bounds. Differences in resource use have long been emphasized in the literature on competition theory (e.g., Chesson 1990). Second, the central quantity is positive only if each consumer has a higher low-density growth rate on one resource type (or equivalently tolerates a lower supply of one resource type; see the appendix and, e.g., Tilman 1982). Finally, we note that the presence of multiple resource types also increases the opportunities for competitive equivalence between consumers (e.g., Lee and Inouye 2010).

The difference between the two bounds in equation (5), generated by consumers' differences in their impact on resources (Chase and Leibold 2003), determines whether opportunities for coexistence exist; we refer to this difference as the size of a coexistence window. The value of the central quantity in equation (5), which represents consumer response to resources (Chase and Leibold 2003), determines whether a given pair of consumer species falls within the coexistence window (e.g., Tilman 1982). To illustrate, consider two consumers that use resources identically (e.g., $u_{ij} = 1$ for all i and j). Then the size of the coexistence window is 0, and coexistence is impossible no matter what the values of the β_{ij}. In contrast, when consumers specialize on different resource stages, for example, when $u_{1J} = u_{2A} = 1$ and $u_{1A} = u_{2J} = 0$, then one bound in equation (5) is 0, and the other is infinite. Because the direction of the inequality signs in equation (5) can change, this means that the size of the coexistence window is infinite: specialist consumers can coexist for any values of the β_{ij} when resource dynamics are consumer independent or do not differ between consumers. Thus, without differences in consumer effects on resource vital rates, at equilibrium different resource stages function as independent resources despite the demographic links between them.

When consumers have different effects on resource demography, population dynamics are more complex, and we analyze them more fully using simulations in the next section. Here we present a simplified case in which, for analytical tractability, the total number of resource individuals is fixed, but consumption by consumer i results in conversion from the juvenile stage to the adult at rate G_i or shrinkage from adult to juvenile at rate S_i. Thus, this scenario includes the essential dynamic feature of consumer-dependent resource transitions. The condition for equilibrium coexistence of two competitors in this case is

$$\frac{S_1}{G_1}\frac{u_{1A}}{u_{1J}} > \frac{\beta_{2A}u_{2A} - \beta_{1A}u_{1A}}{\beta_{1J}u_{1J} - \beta_{2J}u_{2J}} > \frac{S_2}{G_2}\frac{u_{2A}}{u_{2J}} \tag{6}$$

or the same expression with both inequalities reversed (see the appendix for details).
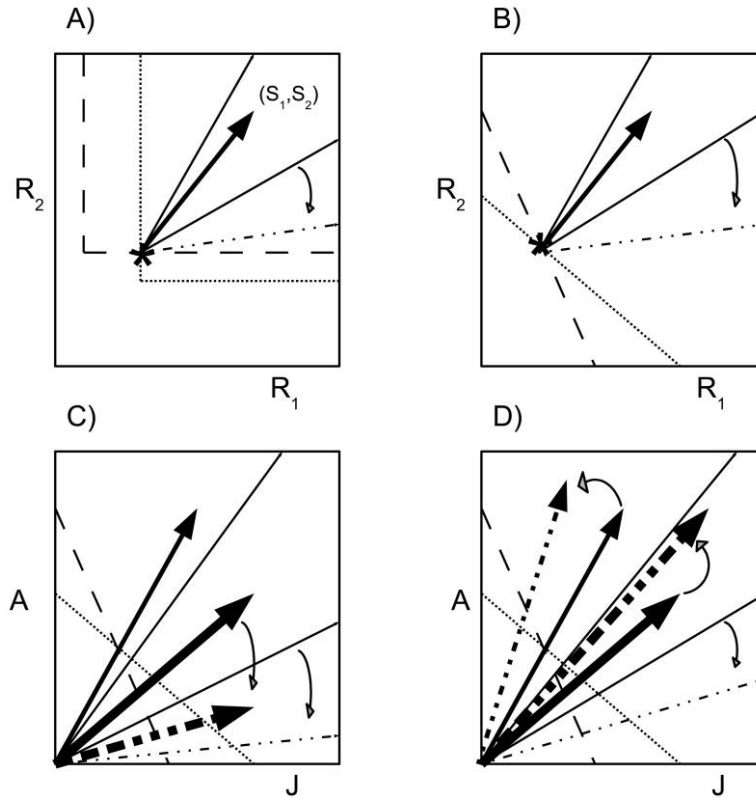
In contrast with equation (5), the right and left bounds

Figure 1: Competition for resources having consumer-independent and consumer-dependent demography and comparison with previous competition models. *A*, Competition for two essential and independent resources (R_1 and R_2), as in Tilman (1982). Competitors draw resources down to equilibrium (asterisk) at the intersection of their zero net growth isoclines (dashed and dotted lines). Coexistence occurs if the equilibrium resource supply vector (arrow) and resource supply point (S_1, S_2) fall inside the region bounded by the slopes of consumption vectors (solid lines). A change in the slope of a consumption vector (curved arrow, dash-dotted line) changes opportunities for coexistence. *B*, Competition for substitutable and independent resources, as in MacArthur (1972). Competitors draw resources down to equilibrium (asterisk) at the intersection of their isoclines. Coexistence occurs if the resource supply vector (but not a resource supply point; see, e.g., Tilman 1982, figs. 75–76, pp. 195–199 for details) falls in the region bounded by slopes of consumption vectors (solid lines). *C*, Competition for dynamically linked resources (juveniles, *J*, and adults, *A*) but consumer-independent resource dynamics (see eq. [5]). Intersection of isoclines is not biologically relevant because consumers generally do not draw resources down; instead equilibrium resource supply occurs at a constant rate (thin solid arrow) determined by equilibrium resource demography (see appendix). Vectors emanate from the origin to emphasize this difference. Coexistence does not depend directly on the resource supply itself (thin solid arrow) but occurs if the resource supply weighted by the ratio of consumers' advantages in single-species low-density growth rates on the different resources (thick solid arrow; see central quantity in eq. [5]) falls in the region bounded by the slopes of consumption vectors (solid lines). A change in the slope of a consumption vector (to the dash-dotted line) changes both the coexistence window and the weights on the resource distribution (dashed arrow). *D*, Competition for dynamically linked resources (juveniles, J, and adults, A) and consumer-dependent resource dynamics. A change in the slope of a consumption vector here affects both the coexistence window and consumers' relative abundance, thereby changing the consumer-dependent resource supply rates (thin solid and dash-dotted arrows). The weighted resource supply vector thus shifts (thick solid and dash-dotted arrows) due to this consumer-mediated change in resource demography as well as changes to its weights, which depend directly on resource consumption rates. The coexistence window also depends on resource vital rates and thus differs (thick and dash-dotted lines) from *C*.

in equation (6) can be different even if consumers use the two resource types equally (or proportionally), provided that the consumers affect resource transition rates in different ways (S_i and G_i). Thus, differences in consumer effects on resource vital rates can enable consumer coexistence in the absence of differences in resource use,

contrary to expectations from consumer-independent theory (eq. [5]). Second, if the consumers are stage specialists (e.g., $u_{1J} = u_{2A} = 1$ and $u_{1A} = u_{2J} = 0$), one of the bounds on the coexistence window can be undefined (e.g., if $G_1 = 0$ or $S_2 = 0$), precluding coexistence. Thus, differences in consumer effects on resource vital rates can
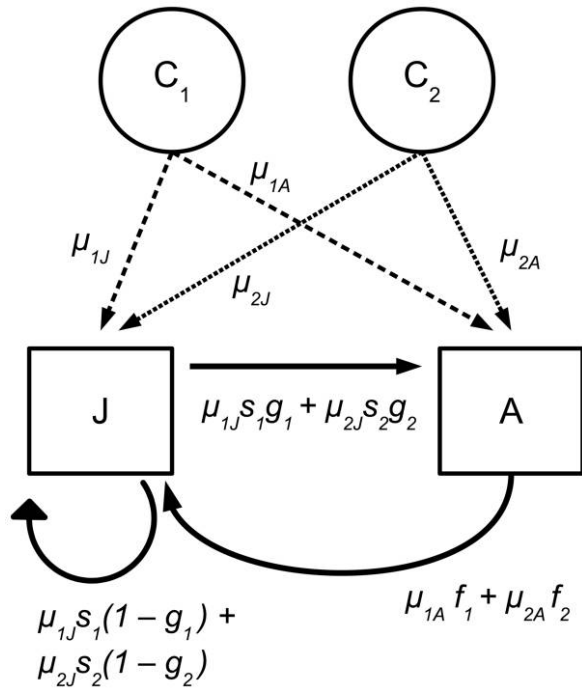
Figure 2: Consumer-dependent resource life history and the consumer-resource relationships explored using simulations. Resource transitions between juvenile (J) and adult (A) stages depend on the juvenile survival (s_i), growth (g_i), and adult fecundity (f_i) rates associated with consumer i (assuming for visual clarity that no resource goes unused). Dashed lines indicate consumption of resources by consumers (C_1 and C_2), with arrows pointing from consumers to resource following graphical convention. Resource uptake fractions μ_{ij} are defined in equations (1) and (2).

guarantee competitive exclusion, even between specialists that use different stages, completely reversing results from consumer-independent theory (eq. [5]). These results reflect the inclusion of nonconsumptive effects in the impact of consumers on their resource (sensu Chase and Leibold 2003). Figure 1 contrasts consumer-independent and consumer-dependent resource demography and compares both to competition for independent resources.

In equation (6), guaranteed exclusion occurs when a consumer completely prevents transitions away from the stage it uses, eventually shifting all resource individuals into its own stage. This extreme result makes intuitive sense, given our simplification of resource dynamics. However, as a result, equation (6) does not allow exclusion between specialists unless it is guaranteed (see the appendix for details); we will use simulation in the next section to show that such possibilities do exist, given more realistic resource population dynamics. The value of the analytic result lies in illustrating the potential power of consumers' effects on resource vital rates relative to resource-use over-

lap and, thus, in demonstrating the importance of determining when to expect coexistence between stage-use specialists in nature.

Differences in consumer effects on resource vital rates alter the dynamics and outcome of competition because they provide a pathway other than simple resource depletion for consumers to affect one another. If, through their effects on resource demography, consumers increase the relative abundance of resource stages favoring their competitors, coexistence is more likely; if consumers' effects instead shift resource structure in a direction disfavoring competitors, exclusion is more likely. Previous competition theory anticipates such a role for nonconsumptive effects on resource availability (e.g., Chase and Leibold 2003, their fig. 2.12); our framework quantifies this role and enables comparison with the role of overlap in resource use.

A More Realistic Resource Life History and Simulation Results

Thus far, we have imposed simplifying assumptions on resource dynamics that help identify mechanisms of coexistence and consumer interaction. Do these mechanisms operate when resource population dynamics are fully articulated in a meaningful life history? We simulate the dynamics of two consumers and a single structured resource, wherein resource vital rates are characteristic of monocarpic plants (fig. 2). Resource projection matrix elements (eq. [4]) consist of consumer-dependent lower-level parameters: growth (g_i), survival (s_i), and fecundity (f_i).

Monocarpic plants survive as nonreproductive juveniles for a variable number of seasons before flowering and dying. This simple life history includes long-lived species as well as short-lived biennials. Although size or other variables may affect juvenile vital rates even in biennials (e.g., Gross 1981), we consider only juvenile and nonpersistent adult stages (fig. 2); we neglect the possibility of a long-lived seed bank. This structure provides a simple but biologically more realistic starting point for considering different herbivores that either exhibit identical patterns of resource stage use or specialize on different plant stages (i.e., feeding on vegetative rosettes or reproductive structures). For example, many monocarpic plants, such as thistles, host insects that specialize as either rosette feeders (consumers of the juvenile stage) or flower-head feeders (consumers of the adult stage; Louda et al. 2005; Takahashi et al. 2009).

Coexistence Despite Complete Resource-Use Overlap

Recall that our consumer-independent results (eq. [5]) always predict competitive exclusion (or competitive neu-
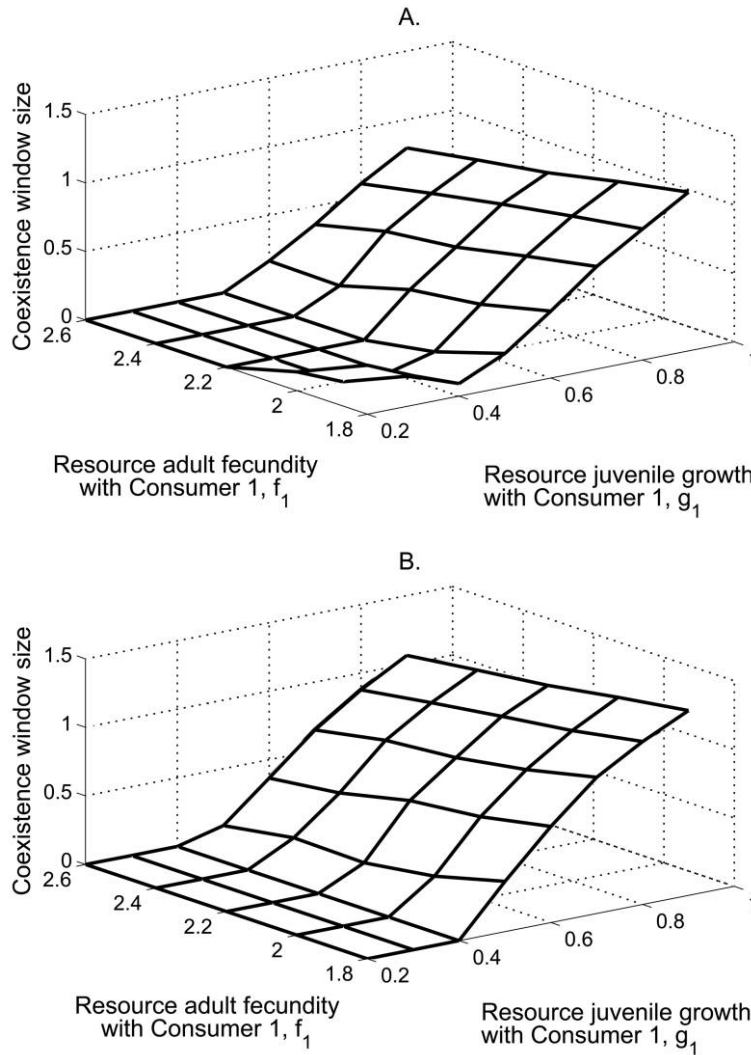
Figure 3: Consumer effects on resource vital rates enable coexistence of consumers despite complete overlap in consumers' use of resource stages. All resource-use parameters $u_{ij} = 1$, and we choose the resource conversion efficiencies β (see the appendix) so that consumer 1 has an advantage on juveniles and consumer 2 on adults. Vital rates due to consumer 2 are fixed at juvenile survival $s_2 = 0.8$, growth to adults $g_2 = 0.5$, and adult fecundity $f_2 = 2.2$. *A*, $s_1 = 0.7$. *B*, $s_1 = 0.9$.

trality at best) when two consumer species use resource stages identically. Figure 3 shows that consumer-mediated resource vital rates can allow competitive coexistence of such consumers, verifying our analytical finding. The figure illustrates the size of the coexistence window. We fix the values of demographic vital rates when plants are used by consumer species 2 and vary the values of vital rates for plants used by consumer species 1. Because our focus here is on demonstrating the possibility of coexistence rather than elucidating the details of its dependence on particular vital rates, we do not dwell on the specific parameter values chosen (given in the figure legend). We

provide greater detail on simulation methods in the appendix.

For the parameter values in figure 3, the size of the coexistence window is nonzero in large portions of the graphs, with coexistence most likely when use by consumer species 1 results in high juvenile growth (g_1) and low adult fecundity (f_1). This promotes coexistence because consumer 1 tends to shift the plant stage structure toward adults, the stage favoring consumer 2 (expressed in βu; see figure legend and the appendix). In figure 3*A*, where plant juvenile survival due to use by consumer 1 (s_1) is lower than in figure 3*B*, the lowest values of g_1 also enable
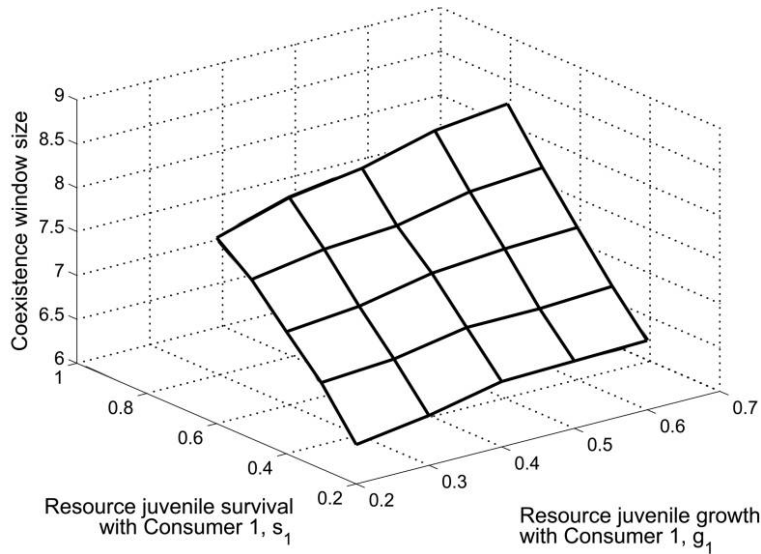
Figure 4: Consumer effects on resource vital rates can prevent competitive coexistence despite complete specialization of consumers on different resource stages. Consumer 1 uses only juveniles, whereas consumer 2 uses only adults ($u_{1J} = u_{2A} = 1$ and $u_{1A} = u_{2J} = 0$); as a result, only the vital rates s_1, g_1, and f_2 affect dynamics. Here, adult fecundity $f_2 = 1.3$; when $f_2 = 2.1$, the graph is almost identical, but the Z-axis ranges from 40 to 50.

coexistence. This second coexistence region is more pronounced at still lower levels of s_1 (not shown). Coexistence under these conditions, in which consumer 1 is extremely detrimental to plant growth and survival, appears to involve two factors. First, consumer 1 favors itself by shifting the resource structure toward juveniles. But second, in our monocarpic resource life history, the resource cannot persist without passing through the adult stage, so that consumer 1 is unable to exclude consumer 2 without negatively affecting its own supply of juvenile plants. As a result, consumer 1 needs a lower advantage (βu) to persist, but consumer 2 does not need to counter with a higher advantage of its own, creating a larger coexistence window.

Although the biological details by which it arises differ between systems, encouraging resource flow to competitors has been explicitly identified as a coexistence mechanism in studies in which competitors consume different pools of a structured resource at different rates (e.g., Farnsworth et al. 2002; de Roos et al. 2008). Here we demonstrate that alteration of the resource structure can also maintain competitors that consume the different resource pools at identical or proportional rates. Identical or proportional resource use is an extreme scenario that may not commonly occur in nature (but see Leibold and McPeek 2006). More frequently, we would expect partial resource-use overlap. Our results indicate that in such cases, consumers' effects on resource vital rates can contribute to coexistence, especially when observed resource

partitioning is insufficient to prevent competitive exclusion. With empirical estimates of key parameters, the relative contributions to coexistence of resource partitioning and consumer-dependent resource vital rates could be quantified.

Exclusion in the Absence of Stage-Use Overlap

As seen in equation (5), results for consumer-independent resource dynamics predict that specialization guarantees competitive coexistence. Figure 4 illustrates that consumer-dependent differences in resource vital rates can result in strong interactions between stage-specialist consumers, such that coexistence is not guaranteed. The coexistence window in figure 4 is larger than in figure 3 yet considerably smaller than the infinite window that results from consumer-independent vital rates (or equality in consumers' effects on vital rates). Because each consumer uses a single resource stage, only a few plant vital rates are germane to system dynamics (here, juvenile growth and survival with consumer 1 and adult fecundity with consumer 2). Nevertheless, these rates have strong effects on consumer coexistence. The coexistence window is smallest when juvenile growth (g_1) and survival (s_1) and adult fecundity (f_2, effects not shown) are low because each consumer species is less likely to shift the plant stage distribution in favor of its competitor. Changing adult fecundity does not change the qualitative pattern of figure

4, but it does change the window size. Juvenile growth has a surprisingly small effect on the coexistence window, especially at low survival values. This is because stage specialists interact only through the stage distribution, and the juvenile specialist affects the abundance of adults primarily through juvenile survival. If survival is low, growth is largely irrelevant. The specific effect sizes shown here depend on the structure of the resource life history; results may differ for nonmonocarpic host plant species.

Interactions between stage-specialized consumers depend on consumers' effects on the resource stage distribution (Haigh and Maynard Smith 1972; de Roos et al. 2008). Competitive exclusion occurs when a consumer is able to drive its competitor's resource below abundances at which the competitor can persist; in contrast with traditional resource competition (e.g., MacArthur 1972; Tilman 1982), a specialist can do this without consuming its competitor's resource stage, due to its effect on resource vital rates (e.g., Briggs 1993; Briggs et al. 1993; Daugherty 2009). An interesting implication is that, in the specific case of stage-specialized herbivores, a consumer can potentially gain a competitive advantage over another consumer by inflicting more nonconsumptive harm on its plant host. Effects of consumer-dependent resource dynamics should also apply to less complete specialization in stage usage, suggesting that unless resource vital rates are independent of consumer identity, indirect interactions between consumers that feed on a structured resource are common.

Discussion

Our results demonstrate that consumers' effects on the vital rates of a shared resource can profoundly affect the dynamics of consumer-resource systems and competitive coexistence. We show that, contrary to familiar expectations based on the use and depletion of independent resources, competitive coexistence can occur in spite of complete resource-use overlap, competitive exclusion can occur in spite of complete resource specialization, and strong interactions are possible between these extremes.

The potential for host plants to mediate indirect interactions among herbivores is widely recognized (Denno et al. 1995; Kaplan and Denno 2007). While most previous work has considered indirect interactions mediated via shifts in plant quality, consumer effects on resource vital rates provide a potentially important but understudied mechanism for such interaction. The dynamics we describe here that are due to herbivore-dependent vital rates involve shifts in not only the population structure of a potentially long-lived resource species but also the population densities of multiple consumer species; these changes may unfold on temporal scales requiring long-term monitoring.

However, given that most plants host multiple herbivores and most herbivores have some demographic impact on their host plants, this pathway of interaction is likely pervasive in nature. Evaluating its importance relative to other direct and indirect interactions is an exciting avenue for further research.

Empirical studies are needed to integrate plant-herbivore systems more fully into the general contexts of consumer-resource interactions and resource competition. Structured demographic models provide a means for translating from resource vital rates and consumer effects on those rates, which can be measured at the individual level, to long-term population structure and dynamics. These tools are already widely accessible and popular for elucidating effects of herbivores on host-plant populations (Halpern and Underwood 2006; Maron and Crone 2006), and they provide an ideal foundation for evaluating long-term, resource-mediated competitive interactions. Additional data are required to estimate resource use and benefit parameters and, thus, link resource demography back to the consumer community.

Previous studies report conflicting results regarding the outcomes of competition between consumers that use different but dynamically linked resource types. In some models, competitive interactions via resource dynamics are strong, and conditions for coexistence are nonexistent or highly restrictive (Briggs 1993; Briggs et al. 1993). In other models, coexistence of resource type specialists is easier to achieve and is sometimes guaranteed (Heard 1994; Wilson et al. 1999; Farnsworth et al. 2002; de Roos et al. 2008; Diaz-Sierra et al. 2010; Lee and Inouye 2010; our study). Our study provides a unifying framework for making sense of these divergent outcomes. In general, coexistence in these different scenarios occurs when consumer activity shifts the resource distribution in favor of competitors, whereas competitive exclusion occurs when consumers reduce availability of competitors' resource types. Because such resource shifts likely alter intraspecific competition relative to interspecific competition, we conjecture that the relative strengths of these two types of competition predict competitive outcomes (Chesson 2000).

Both the effect of the consumers on the resource (eqq. [3], [4]) and the effect of resources on consumers (eq. [2]) depend on the fraction of each resource consumed by each species ($\mu_{ij}(t)$); recall that these fractions are linear functions of the consumer species' relative densities (eq. [1]). In situations in which each individual of the resource population associates with only one consumer species during one time interval, such as in many ant protection mutualisms (e.g., Miller 2007), the $\mu_{ij}(t)$ represent the proportions of resource individuals associating with each consumer species. In other situations, such as in plant-herbivore and host-parasite interactions, a single resource

individual may experience joint use by multiple consumer species in one time interval. Our model represents the demographic effect of joint consumption as a linear, additive function of the effects of each consumer. Empirical studies show that effects of different consumers may interact (e.g., Morris et al. 2007), but because these same studies indicate that interactions are likely to be system specific, we use the linear and additive assumption as a useful starting point that enables comparison to classic competition models. Future work will investigate nonlinearity in resource capture (via changes in the $\mu_{ij}(t)$) and greater complexity in consumer effects on or responses to their resource (via changes to the m_{ikj} or β_{ij}, respectively).

Our models assume a simple form of density dependence in the resource (eq. [3]) that does not alter the relative abundances of resource stages. This has enabled us to focus on the critical role of consumers' effects on resource stage structure in competitive coexistence and exclusion. Density dependence is unlikely to be so simple in natural systems, however, and we fully expect that stage-specific density dependence could be an important factor in competitive dynamics (as in de Roos et al. 2008). Further, the life history we have considered for the resource species (fig. 1) is appropriate for monocarpic plants, some insects, and other possibilities, but we expect that more complex resource life histories would result in richer dynamics. The MacArthur-type consumer-resource framework on which we base our model allows for multiple resources and would easily accommodate more resource stages. In fact, a natural next step may be to consider the resource population to be structured by a continuous variable such as size, rather than dividing it into discrete stage classes (e.g., Easterling et al. 2000; Ellner and Rees 2006). Our purpose in de-emphasizing life-history complexity, density dependence, and other potentially important factors in this study has been to demonstrate the essential dynamic consequences of consumers' effects on resource demography, which are best illustrated in simple cases. Our model provides a starting point for examining whether and how additional biological details can interact with the core pathway of consumer interaction via resource vital rates.

Our discrete-time MacArthur-type model of competition describes consumer-resource relationships in which individuals do not continuously interact over multiple time periods. Interactions such as those between pollinators or frugivores and individual plants fall into this category, as do ant protection mutualisms in which ant colonies may protect individual plants through a season or a year but display little or no territorial attachment on the temporal scale of multiple reproductive events for either plants or ant colonies. These contrast with systems in which long-term relationships do form, necessitating

different models for the underlying competitive dynamic between consumers. For instance, in obligate ant protection mutualisms, ant colonies may occupy individual host plants for several years, which can span several generations of both ant colonies and plants; a lottery model of competition is most appropriate in such cases (Lee and Inouye 2010). These differences in relative temporal scales have important ecological implications. Consumer-dependent resource vital rates alone (in the absence of stage structure) can enable stable coexistence in lottery competition due to an underlying acquisition-retention trade-off (Lee and Inouye 2010), whereas resource stage structure is necessary for stable coexistence in shorter-lived consumer-resource interactions. Thus, we can think of these different frameworks for competition models (lottery vs. MacArthur type) as the endpoints for a temporal-scale continuum, covering systems in which competitors' effects on their resources are not limited to outright consumption.

Early competition theory focuses on resource consumption as the means by which competitors influence each other indirectly (e.g., MacArthur 1972; Tilman 1982). More recent theory generally (e.g., Chase and Leibold 2003) or specifically (e.g., Briggs 1993; Wilson et al. 1999; Farnsworth et al. 2002; Murdoch et al. 2003; de Roos et al. 2008; Daugherty 2009; Diaz-Sierra et al. 2010; Lee and Inouye 2010) acknowledges the ubiquity and importance of effects on resource dynamics. We have presented a novel model framework that integrates effects of consumers on the vital rates of their resources with classic resource-use theory, enabling quantitative comparison of the relative importance for competitive coexistence or exclusion of both resource use (or consumption per se) and nonconsumptive manipulation of resource dynamics. We focus here on herbivores, but our approach identifies principles that should apply to diverse competitive systems including parasites, parasitoids, pathogens, and mutualists. The modeling readily extends to a range of other resource states among which transitions can be defined, such as trait-mediated indirect interactions involving host nutritional quality or defensive status, or spatial systems in which resource individuals move between habitats in response to consumer attack. Finally, by considering consumers that might use the same resource population very differently (e.g., leaf-feeding herbivores, meristem borers, and seed predators), our work extends quantitative competition theory to encompass consumers in different feeding guilds or taxonomic groups. Thus, we are optimistic that application and testing of the theory presented here will promote a comprehensive synthesis of competitive interactions in a wide range of biological contexts.

Acknowledgments

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