

Mutualism between Consumers and Their Shared Resource Can Promote Competitive Coexistence

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Submitted March 4, 2009; Accepted October 11, 2009; Electronically published January 25, 2010

Online enhancement: appendix.

ABSTRACT: Competitive coexistence depends on dynamic interactions between competitor and resource populations, including mutualism between the resource and each competitor. We add mutualism to a well-known model of resource competition and show that it can powerfully stabilize competitive coexistence in the absence or presence of resource heterogeneity. We use a transition matrix approach to describe lottery competition, while allowing each of two competitors to affect the population dynamics of their shared resource. For example, two plant-defending ant species may compete for nesting space within ant-adapted (myrmecophytic) plants. We show that mutualism between consumers and a resource species can stabilize competitive coexistence of the consumers by allowing each competitor to influence resource dynamics in a way that benefits the other. The effect of this novel coexistence mechanism depends on a mutualism's biological details: for example, altering myrmecophyte fecundity affects competing ant species differently than does altering plant survival. Finally, we consider a heterogeneous resource (e.g., two types of nest site) and show how niche partitioning can stabilize coexistence in the absence of resource dynamics. When resource heterogeneity is dynamic (e.g., small and large plants of the same species), niche partitioning also provides new routes for additional stabilization via mutualism.

Keywords: competition, mutualism, demographic structure, niche differentiation, lottery model, myrmecophytes.

Introduction

Understanding the mechanisms that contribute to the coexistence of competing species is one of the central goals of ecology. Positive interactions, which are widespread and important components of ecological communities (Bronstein 1994; Bruno et al. 2003), have the potential to alter the dynamics of resource competition. Until recently, consideration of mutually beneficial interactions has focused on species pairs, but recognition is growing that mutualisms can be viewed within the broader framework of

consumer-resource interactions (Holland et al. 2005) and exist within ecological webs that also include competition (Stanton 2003; Thompson 2005; Okuyama and Holland 2008). Competition between members of a guild for their mutualistic partner as a shared resource is an excellent test case for the study of the interaction between competition and mutualism (e.g., Cushman and Addicott 1989; Palmer et al. 2003).

Existing analyses of the ecological dynamics of competition and mutualism focus on the persistence of a mutualistic pair in the presence of a cheater (e.g., Marr et al. 2001; Bronstein et al. 2003; Hoeksema and Kummel 2003; Morris et al. 2003; Wilson et al. 2003), such as an obligate plant-pollinating seed parasite mutualism exploited by a seed predator that does not provide pollination services (Pellmyr et al. 1996). These studies begin by assuming that competitors differ in provision of services and frequently also in competitive ability. Therefore, these analyses do not compare systems with mutualism (i.e., positive effects of consumers on the resource) to those without, which could be described by a classic competition model. Here we make this comparison to describe how mutualism alters known mechanisms of competitive exclusion or coexistence. We incorporate mutualism in a way that allows consumers to influence resource attributes as well as resource abundance. Thus, our framework unites not only the study of mutualism and competition but also the study of density-mediated and trait-mediated competitive interactions.

The models that we develop here are applicable to many species, but we will discuss them in the context of a biological example to illustrate how model components relate to an empirical system. Our specific interest is interactions between ant-adapted plants (myrmecophytes) and the ant species that patrol and protect them. These occur in a wide range of plant and ant taxa and are found in semitropical and tropical areas around the world (reviewed in Heil and McKey 2003). In terms of model structure, the key biological feature of these systems is that com-

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petitors defend or occupy long-lived resources through multiple seasons. We combine territorial defense with mutualistic influence of consumers on the resource using a matrix approach that describes transitions in consumer occupancy of resource individuals and that readily incorporates resource population structure. Other long-term mutualisms include plant-fungal endophyte mutualisms, digestive symbioses, plant-rhizobial interactions, and other two-way consumer-resource mutualisms (Holland et al. 2005). Our main conclusions, however, do not require a close match to the biology of these systems; for example, because our models allow for harmful effects of competitors on their resource, our results also have important implications for competition between parasites or different strains of some diseases.

The full spectrum of consumer-resource feedbacks includes resource populations that are structured by size, stage, infection status, or other classes. As a first step toward incorporating resource demographic structure, we extend the application of lottery models to cases with two dynamically linked resource types and investigate how competitive coexistence depends on the distribution of resource states. Although this new extension of lottery theory is motivated by our interest in mutualistic feedbacks between consumers and resource dynamics, its results hold implications for any competition for a structured resource and are not limited to mutualisms. To introduce the core dynamics, we will first analyze static resource heterogeneity, where resource types are independent of one another.

In “Biological Context, Model Framework, and Classic Lottery Dynamics,” we use the context of ant-myrmecophyte mutualism to present our model framework. We then include resource (myrmecophytic plant) demography, with survival and reproduction determined by the different mutualist (ant) species; we generally assume that the consumers benefit the resource to different extents (e.g., Bruna et al. 2004; Frederickson 2005; Miller 2007; Young et al. 2008), but this framework also allows for these species to harm the resource (e.g., Yu and Pierce 1998; Stanton et al. 1999; Yu 2001; Izzo and Vasconcelos 2002). In other words, a competitor can be a cheater, providing no benefits to a plant (Janzen 1975) or even negatively affecting it. We show that competitors’ influences over resource vital rates permit coexistence over large regions of parameter space. Resource heterogeneity also increases the capacity for coexistence, and mutualism can then additionally contribute to stabilization through shifts in resource demographic structure. In general, the stabilizing effect of mutualism arises when each competitor shifts the resource population in a way that benefits the other species or in a way harmful to itself.

Biological Context, Model Framework, and Classic Lottery Dynamics

In ant-myrmecophyte mutualisms, multiple ant species may compete for access to domatia, which are specialized plant structures in which ants establish colonies (e.g., Davidson et al. 1989; Gaume and McKey 1999). In return for nesting space, ant colonies protect their host plant from herbivores and/or competitors, which can lead to increased plant survival, growth, and reproduction (e.g., Vasconcelos 1991). These benefits may feed back to affect the number and type of plants available to ants, altering the dynamics of competition between ant species (Frederickson and Gordon 2009). In many ant-myrmecophyte systems, displacement of ant colonies does not occur (but see Palmer et al. 2002; Palmer 2003): a colony must die before a queen can found a new colony on the same plant. Competition for open nesting spaces and lack of displacement of established colonies characterize lottery competition (Yu and Wilson 2001). In the absence of stabilizing factors such as environmental variability, the lottery model is capable of at best neutral dynamics (Chesson and Warner 1981; Warner and Chesson 1985), which we will describe more fully. We ask whether feedbacks between competitors and a shared resource, such as between ant species and a shared obligate myrmecophyte host, and/or resource structure can broaden opportunities for competitive coexistence (fig. 1).

Transition Matrix Approach

Because competitors can have different effects on resource vital rates, we consider the resource to be structured by consumer occupancy, whether or not it is additionally structured by size and/or stage. Myrmecophytic ants, which are typically obligate mutualists, can nest only in plants, so given a fixed number of ant colonies per plant (we assume one), there is no need for separate equations to describe consumer abundance. We define a projection matrix, $\mathbf{M}(t)$, that describes transitions between resource types and therefore also changes in the abundance of consumer species. Plant transitions can occur via turnover in ant species and via plant growth and fecundity. Plant dynamics are density dependent, keeping plant and ant abundance finite at equilibrium and avoiding runaway mutualist populations (May 1981). We assume that total density affects all plants equally, so that density dependence does not affect the distribution of resource types. The specific functional form of density dependence in the plant is thus not important to the competition between the ants; here we use a Ricker function. Then plant and ant dynamics are given by

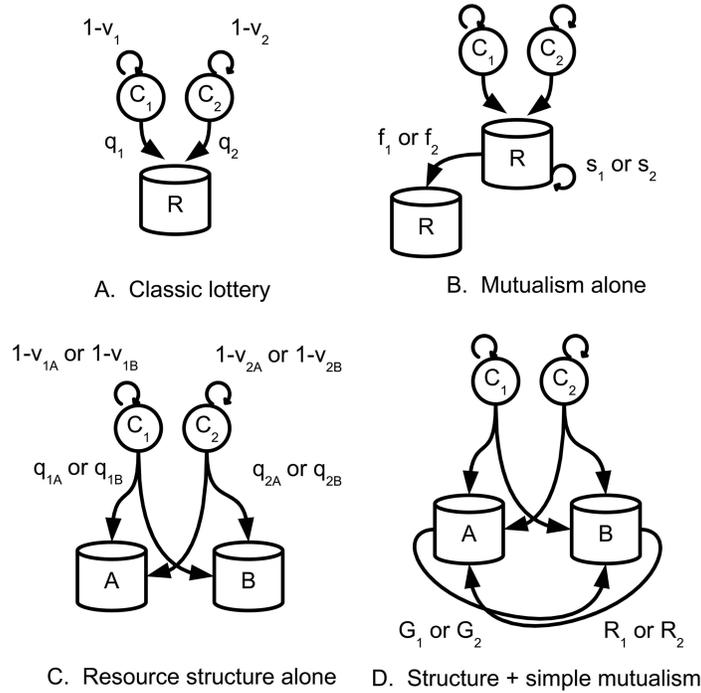


Figure 1: Interspecific interactions in each scenario considered. A, Classic lottery system: two consumers (C_1 , C_2) compete for resource R . For ants competing for nesting space, relevant vital rates are the rate of queen production per colony (q_x) and colony death rate (v_x). The probability of gaining access to the resource is the proportion of queens belonging to each ant species. B, We add mutualism between the consumers and the resource by allowing individual plants to survive (s_x) and reproduce (f_x) at rates dependent on which ant species occupies them. Consumers behave as in A. C, We add resource structure to the classic lottery system by allowing two types of nesting space. Now consumer vital rates depend on what type of resource each colony occupies, but queens do not distinguish between the two types. D, Resource structure and simplified mutualism dynamics are added together by allowing transitions between the two resource types at rates G_x and R_x , depending on which ant species is resident. Consumers behave as in C.

$$\mathbf{n}(t+1) = \mathbf{M}(t)\mathbf{n}(t)e^{-rN(t)}, \quad (1)$$

where $\mathbf{n}(t)$ is a vector of plant numbers in each size or stage class occupied by each ant at time t and $N(t) = \sum \mathbf{n}(t)$ is the total population size at time t .

Following the classic lottery assumption (Sale 1977; Chesson and Warner 1981), an ant species colonizes an unoccupied plant with probability equal to the proportion of that species' queens among all queens seeking host plants. With two ant species, the probability of occupancy by ant species 1 is

$$\begin{aligned} R_1(t) &= \frac{Q_1(t)}{Q_1(t) + Q_2(t)} \\ &= \frac{\sum_1^k q_{1,i} n_{1,i}(t)}{\sum_1^k q_{1,i} n_{1,i}(t) + \sum_{k+1}^{2k} q_{2,i} n_{2,i}(t)}, \end{aligned} \quad (2)$$

where k is the number of plant size or stage classes, $q_{x,i}$ is the number of queens of species x produced by a colony

on a plant in class i , and $Q_x(t)$ is the total number of queens of species x at time t . The indices of $n_{x,i}(t)$ indicate that within the $2k \times 1$ column vector $\mathbf{n}(t)$ are two blocks, each a column vector k long. Plant transitions between ant species depend on occupancy probabilities, which we indicate by writing $\mathbf{M}(t) = \mathbf{M}(P(t))$. This together with equations (1) and (2) defines a nonlinear projection matrix, as in every time step the rules for population change depend on the current status of the population (for analysis of a similar nonlinear system, see Lee and Tuljapurkar 2008).

Let $\mathbf{n}(t) = N(t)\mathbf{u}(t)$, so that the vector $\mathbf{u}(t)$ describes the proportion of plants in each state (plants of each size or stage class occupied by ant species 1 or by ant species 2). Then equation (1) implies that at equilibrium,

$$\hat{\mathbf{u}}e^{r\hat{N}} = \hat{\mathbf{M}}\hat{\mathbf{u}}, \quad (3)$$

where a hat accent denotes an equilibrium quantity. Equation (3) identifies $e^{r\hat{N}}$ with the dominant eigenvalue λ of

the equilibrium matrix \hat{M} and the equilibrium structure vector \hat{u} with the corresponding right eigenvector. From the dominant eigenvalue, we can determine the total population size at equilibrium, and from the corresponding eigenvector, we obtain the relative abundances of the resource states. Summing within consumer types yields the equilibrium relative abundances of the competitors; the relative abundances together with the total abundance yield the individual equilibrium densities. Thus, properties of the equilibrium matrix alone provide the solution to the density-dependent equation.

*Dynamics in the Absence of Mutualism
or Resource Structure*

We can use our transition matrix approach to reproduce previous results for the classic lottery model (Chesson and Warner 1981), which describes competition for a fixed number of nesting spaces (fig. 1A). This validates the model framework and establishes the starting point to which we will add ant-plant mutualism and plant stage structure. Details of the analysis appear in the appendix in the online edition of the *American Naturalist*; here we summarize the dynamics. For two species in lottery competition, one consumer almost always excludes the other, and stable coexistence (where some mechanism prevents exclusion of either species) is impossible. However, certain precise conditions result in neutral dynamics, where, bar-

ring perturbations, the species' initial abundances remain unchanged: if both species are present initially, they both persist indefinitely. In a finite population, neutral dynamics result in a random walk in the species' relative densities. If the probability of ant colony death in one time step is v_x for species x , we can show that neutral dynamics occur when $q_1/v_1 = q_2/v_2$, just as is shown by Chesson and Warner (1981). The two competitors must be equal in the rate at which they gain nest sites (q_x) relative to the rate at which they relinquish them (v_x). Thus, in classic lottery competition, competitive exclusion is avoided only if a delicate and unlikely balance of the colony birth and death rates of the two species leads to neutral dynamics (scenario A in table 1).

These properties of lottery competition are a critical component of the mechanism by which mutualism will increase opportunities for coexistence. An ant species that cannot retain occupied plants (high v_x) can compensate by producing many queens to gain new plants, and vice versa. Neutral dynamics do not require the two ant species to be identical in both rates: one can have an advantage in plant acquisition and the other in plant retention, as long as the two advantages balance precisely. This acquisition-retention trade-off is reminiscent of a colonization-competition trade-off in systems where displacement occurs, but the competition-colonization trade-off can alone allow stable coexistence because the possibility of competitive displacement effectively divides the resource pop-

Table 1: Summary of scenarios considered and conditions for neutral dynamics in each

Scenario and conditions for neutral dynamics	Interpretation	Stable coexistence
A. Classic lottery $q_1/v_1 = q_2/v_2$	Acquisition-retention trade-off	No
B. Mutualism alone Option 1: $q_1 = q_2, s_1(1 - v_1) = s_2(1 - v_2)$ Option 2: $f_1 - f_2 = s_2 - s_1, q_1/(f_1 + s_1v_1) = q_2/(f_2 + s_1v_2)$	Acquisition and retention each balance; resource supply does not matter Effects on resource supply cancel; acquisition-retention trade-off includes plant vital rates	Yes
C. Resource structure Option 1: $q_1/v_1 = q_3/v_3, q_2/v_2 = q_4/v_4$ Option 2: $v_1/v_2 = v_3/v_4 = (1/A)[(q_3v_1 - q_1v_3)/(q_2v_4 - q_4v_2)]$	Acquisition-retention balance within each resource type Acquisition-retention advantages balance across resource types, taking relative abundance of types into account	Yes
D. Structure + simple mutualism Option 1: $q_1/v_1 = q_3/v_3, q_2/v_2 = q_4/v_4, q_1/v_1 = q_2/v_2, q_2/v_2 = q_3/v_3, q_3/v_3 = q_4/v_4, q_1/v_1 = q_4/v_4$ Option 2: ^a $G_2v_1/R_2v_2 = G_1v_3/R_1v_4 = (q_3v_1 - q_1v_3)/(q_2v_4 - q_4v_2)$	Acquisition-retention balance within and across stages; plant rates do not matter; see option 1 in scenario C At least one criterion involving plant rates; leading terms analogous to option 2 in scenario C	Yes

Note: See figure 1 for a graphic representation of the four scenarios. Model parameters are as follows: q_x is queen production rate, and v_x is the rate at which colonies vacate plants (i.e., colony death rate), where the subscript indicates ant species in A and B; in C and D, subscripts 1 through 4 indicate ant species 1 on the first and second plant type and ant species 2 on the first and second type, respectively. Plant fecundity is f_x , and plant survival is s_x , where the subscript indicates ant species; A is the ratio of resource type abundances in C, and in D, G_x and R_x are ant-mediated rates of change from the first plant type to the second (juveniles to adults) and back, respectively. The last column indicates whether stable coexistence is also possible in each scenario; conditions for stable coexistence are discussed in the text.

^a See appendix.

ulation into two segments, unoccupied and occupied resources, on which two competitors can specialize. When displacement does not occur, acquisition and retention of the single resource are only opposite sides of the same coin (Yu and Wilson 2001). Though the acquisition-retention trade-off cannot therefore allow stable coexistence, it is the underlying process that allows mutualistic feedbacks between the ant species and their plant resource to do so.

Mutualism Promotes Coexistence

Multiple Ways to Be a Mutualist, Multiple Ways to Coexist

We incorporate mutualism by allowing plant vital rates to depend on which ant species occupies and patrols the plant; we let plant mortality be $1 - s_x$ and fecundity be f_x (fig. 1B). Thus, the two ant species may differ in their effects on the plant (e.g., Bruna et al. 2004; Frederickson 2005). The resulting transition matrix is shown in the appendix. The equilibrium abundance of ant species 2 relative to that of species 1 is

$$\hat{u}_2 = \frac{q_1(s_1 - s_2 + f_1 + s_2v_2) - q_2(f_1 + s_1v_1)}{q_2(s_2 - s_1 + f_2 + s_1v_1) - q_1(f_2 + s_2v_2)}. \quad (4)$$

Seeking situations where $\hat{u}_2 = 0/0$ (i.e., is undefined; see appendix) reveals conditions for neutral dynamics, which are given in scenario B in table 1. We see that mutualism increases the opportunities for neutral dynamics from one in the basic lottery model to two, and we will show that it also makes stable coexistence possible. To clarify how mutualism can facilitate coexistence, we first explain how resource population dynamics participate in the interaction between competitors.

Resource fecundity and survival both affect the supply of unexploited resource individuals. Fecundity creates new plants, whereas survival of a plant beyond the demise of its ant colony makes a plant newly available for colonization. Increasing the supply of unexploited resources favors resource acquisition over resource retention. Survival may seem less important in this respect than fecundity because plant survival is assured in the basic model, but we will see that the two processes are equally important. While survival of an unoccupied plant favors plant acquisition, survival of occupied plants favors the resident ant colony, assuming that a colony dies if the plant it occupies dies. Thus, in addition to its acquisition-specific aspect, plant survival directly benefits the resident ant species and, in this sense, functions similarly to the ant traits of queen production and colony survival.

The different roles of the two resource vital rates interact with consumer vital rates. We see in scenario B in table 1

that both trade-offs producing neutral dynamics involve not only the ant traits, q_x and v_x , but also an ant colony's influence on at least one plant trait, s_x or f_x . In the first alternative in scenario B in table 1, an ant-mediated increase in plant fecundity has no effect, while in the second, it is detrimental to the species responsible. Further, each alternative emphasizes a different aspect of survival, with survival of occupied plants appearing in the first criterion and survival of vacated plants in the second. Finally, the acquisition-specific effects of ant species on plant fecundity and survival cancel each other in the second criterion. Because of these combined effects of competing species' traits and their effects on their shared resource (part of a species' extended phenotype), substantial life-history differences between competitors may still result in neutral dynamics. The presence of life-history differences need not automatically be interpreted as an indication of stable coexistence via life-history trade-offs.

The prevalence of neutral dynamics in nature is a matter of debate (e.g., Hubbell 2006; Leibold and McPeck 2006), but if they are important, doubling the ways to achieve them is a biologically significant consequence of mutualism between consumers and their shared resource. We emphasize again that although alternative neutral combinations are equivalent in fitness, they may be distant from each other in life-history parameters; this could be important in evolutionary modeling, which frequently assumes that competing strategies are nearby in parameter space. Finally, any mechanism that stabilizes coexistence does so in the face of inequality between competitors (Chesson 2000; Leibold and McPeck 2006): the more nearly equal competitors are in fitness, the less strong a stabilizing mechanism needs to be to guarantee coexistence. Thus, in combination with any other stabilizing factor, including spatial or temporal heterogeneity, trade-offs that broaden the opportunities for neutral dynamics can contribute indirectly to the likelihood of achieving stable coexistence.

If \hat{u}_2 is positive and finite, then the consumers' equilibrium abundances depend not on initial abundances but on competitor and resource vital rates. We can write the conditions when this occurs as constraints on the relative queen production rates of the competitors,

$$\frac{f_1 + s_1v_1}{s_1 - s_2 + f_1 + s_2v_2} > \frac{q_1}{q_2} > \frac{s_2 - s_1 + f_2 + s_1v_1}{f_2 + s_2v_2}, \quad (5)$$

or the same expression with the direction of both inequalities reversed. With other parameters fixed, coexistence requires not a precise value for q_1 but rather any of a range of values within a window: the ratio of queen production rates must lie between the bounds in equation (5). If this ratio exceeds the upper limit, then species 1

excludes its competitor, and if less than the lower limit, then species 2 wins. When coexistence is stable, the relative abundances of the ant species approach ($\hat{u}_1 = 1, \hat{u}_2$) from any initial conditions that include both competitors. Ant species abundances may fluctuate around the equilibrium as a result of the lagged density dependence intrinsic to the discrete time formulation, or in some cases the plants (and thus both ants) may become extinct, but neither competitor excludes the other.

To understand how mutualism can stabilize coexistence, we first focus on the role of plant fecundity by setting the competitors' effects on plant survival equal, $s_1 = s_2 = s$. (Some examples in which differences in competitors' effects on their resource may primarily involve fecundity are discussed in "Cheaters Do Not Necessarily Exclude Mutualists.") The conditions for coexistence simplify to

$$\frac{f_1 + sv_1}{f_1 + sv_2} > \frac{q_1}{q_2} > \frac{f_2 + sv_1}{f_2 + sv_2}, \quad (6)$$

or the same expression with both inequalities reversed. The bounds on the queen production ratio are equal if $f_1 = f_2$ or if $sv_1 = sv_2$, so stable coexistence requires differences in colony death rates as well as in the ants' effects on plant fecundity. Inequality of both rates is necessary because plant fecundity has acquisition-specific effects and requires an underlying acquisition-retention trade-off in order to participate in the consumers' interaction. If the ant species whose occupancy leads to higher plant fecundity is also a better colonizer of new vacant plants, then if it becomes more abundant through an overall q/v advantage, it leads to production of more new plants and continues to increase through a positive feedback. The feedback is instead negative if the ant species that acquires plants better but retains them less well also leads to lower plant fecundity: if this ant species increases in abundance, the empty plants on which it thrives decrease. Thus, plant fecundity provides a pathway for frequency dependence that can either destabilize or stabilize the competitors' relative abundance. Simulations (not shown) confirm that coexistence is stable when $\Delta f = f_2 - f_1$ and $\Delta v = v_2 - v_1$ are of opposite sign; the equilibrium is unstable if the differences are of the same sign. Note that stable coexistence means that the ant species that is a better mutualist partner from the plant's perspective (i.e., has a larger positive effect on plant fecundity) persists in the presence of a less beneficial competitor.

Our results demonstrate that mutualistic consumer-resource feedbacks can prevent competitive exclusion despite an imbalance in the competitors' q/v ratios and that stronger negative feedbacks can counteract larger imbalances. Figure 2 shows that greater differences between the competitors' effects on plant fecundities and colony death

rates promote stable coexistence more strongly. The dependent variable is the range on the queen production ratio (or, equivalently, the range on q_1 as a proportion of q_2) from equation (6). The rates associated with ant species 2 are fixed; opportunities for stable coexistence exist if ant species 1 either has a lower colony death rate ($v_2 - v_1 > 0$) and leads to higher plant fecundity ($f_2 - f_1 < 0$) or has a higher colony death rate and causes lower plant fecundity. These two possibilities are the two positive quadrants of $(\Delta v, \Delta f)$ space in the figure; we have set the other two equal to 0 because the equilibrium is unstable in these quadrants. Colony vacancy rates are bounded by 0 and 1, but the competitors' effects on plant fecundity are limited only by biological feasibility.

When $s_1 \neq s_2$, we see from equation (5) that coexistence is possible even if $f_1 = f_2$ and $v_1 = v_2$. A mutualism that reduces plant mortality is thus qualitatively different from a mutualism that increases plant fecundity. Differences in plant survival rates alone can allow stable coexistence because the resident-specific and acquisition-specific effects of plant survival act as ant colony death rate and plant fecundity do together, and even with all other traits equal, stable coexistence is possible as long as the ant species with lower plant survival also produces more queens. If we also allow the v_x and f_x to differ, stability depends on the precise values of Δs , Δf , and Δv . Stable coexistence is most likely when all three parameters enhance the acquisition-retention trade-off between the ant species and the negative feedback of each ant on itself, with one species having a high vacancy rate and lower plant survival and fecundity and the other species having a low colony death rate and providing high plant performance. Figure 3 shows that the resulting range of queen production in ant species 1 can be larger than q_2 under these conditions.

Cheaters Do Not Necessarily Exclude Mutualists

We have seen that mutualism can allow stable persistence of mutualists that differ in the quality of services provided. To follow up on this point, we consider the special case in which one ant species is detrimental to the plant, reducing it to very low fecundity and also substantially lower survival than its competitor. This cheater harms itself through the resident-specific disadvantage of low plant survival and cannot compensate by acquiring new plants because it also leads to low plant fecundity. Thus, unless its competitor vacates plants very quickly (in which case, criterion [5] applies), the cheater cannot exclude its competitor. In fact, it is always competitively excluded unless it produces enough queens to colonize new plants quickly (a result anticipated in Janzen 1975). Specifically, we can show that if species 1 is so harmful to the plant that $s_1 - s_2 + f_1 + s_2 v_2 < 0$, then it is excluded unless

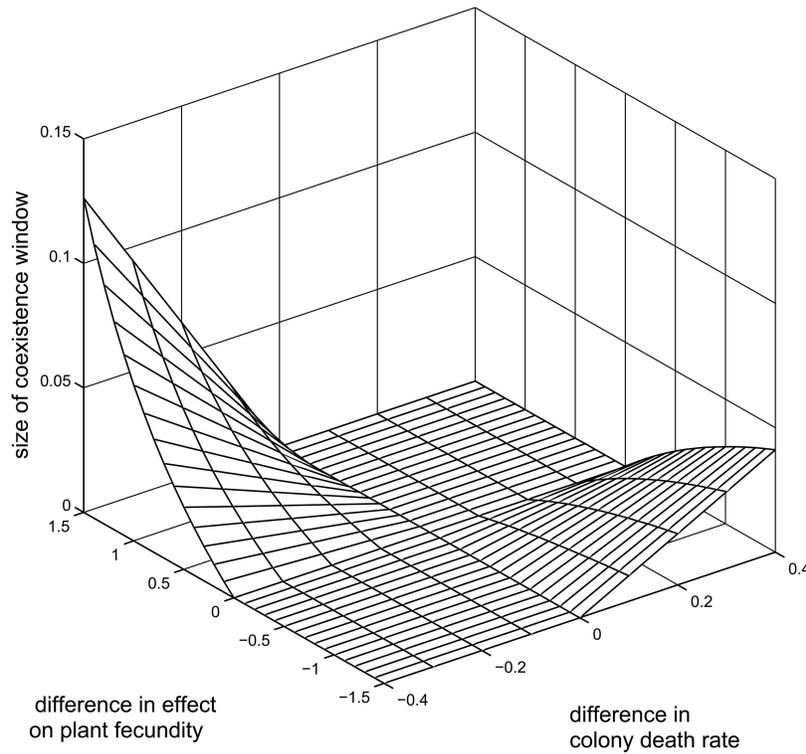


Figure 2: When competitors' effects on plant survival are equal, differences in their effects on plant fecundity and their colony death rates can promote stable coexistence. The size of the stable coexistence window (range on the queen production rate of ant species 1, q_1 , as a proportion of its competitor's queen production rate, q_2) is shown as a function of the difference in the ants' effects on plant fecundity, $\Delta f = f_2 - f_1$, and in their colony death rates, $\Delta v = v_2 - v_1$. Rates for species 2 are fixed ($q_2 = 3$, $v_2 = 0.5$, $f_2 = 2.5$, $s_2 = 0.9$), and $s_1 = 0.9$, where s_x is the survival rate of the plant when occupied by ant species x .

$$\frac{q_1}{q_2} > \frac{s_2 - s_1 + f_2 + s_1 v_1}{f_2 + s_2 v_2}. \quad (7)$$

Thus, while cheaters may frequently be assumed to be competitively superior because they do not incur the costs of providing mutualistic services, a cheater can have both a higher queen production rate and a lower vacancy rate but still fail to exclude its competitor. Very high queen production by the cheater can lead to plant extinction unless the competitor is a strong enough mutualist, but competitive exclusion does not necessarily precede system collapse. The extent of harm allowed by our cheater is extreme; however, Janzen (1975) reports that acacia trees typically die within a year of being colonized by an ant species that fails to protect plants (but see Moraes and Vasconcelos 2009).

“Castrating” ants that have negative effects on plant fecundity (e.g., Yu and Pierce 1998; Stanton et al. 1999; Izzo and Vasconcelos 2002) may appear to cheat in a way that is not self-detrimental, and some authors have argued that ant colonies should defend only the plant structures

that contribute directly to the performance of the occupying colony (e.g., Yu and Pierce 1998; Palmer and Brody 2007). Our analysis clarifies that any competitive advantage of such strategies depends on the life-history traits and constraints of the cheater, the competitor, and the resource as well as on ecological context. For example, influencing resource traits can destabilize coexistence, but this is advantageous to a consumer only if it already enjoys an acquisition-retention advantage. Castration activities could carry an energetic cost, while the effect of nonpatrolling of specific plant structures would depend on the abundance and behavior of plant enemies. Since some mutualists do protect resource fecundity (e.g., Vasconcelos [1991] found a 45-fold decrease in fruit production by a myrmecophyte following ant removal), explicit quantification of the consumer and host vital rates is necessary to understand how mutualism affects competition between consumers.

Our analysis also applies directly to parasites and to diseases that can reinfect recovered hosts, although in these cases the mutualist-cheater labels do not apply. Our focus

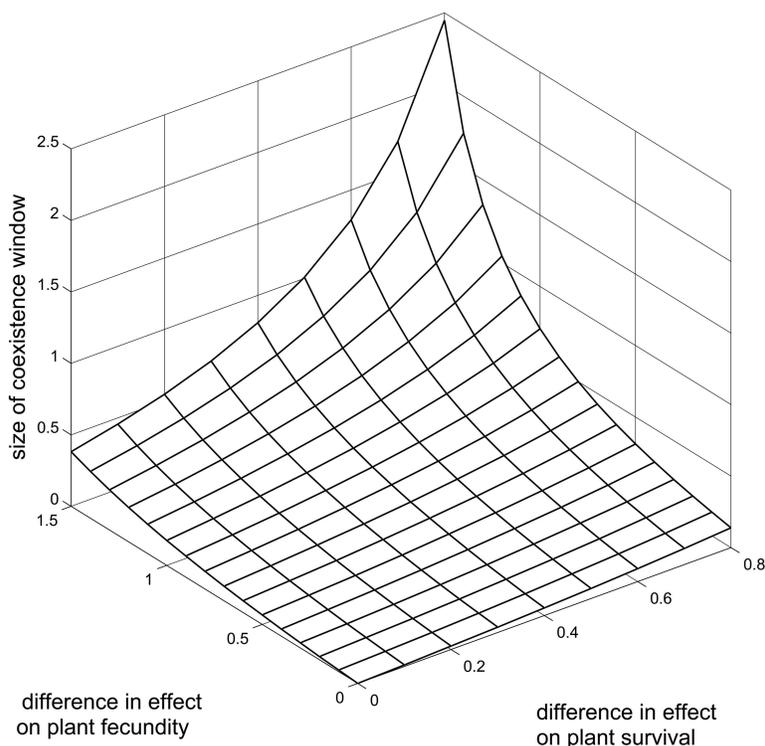


Figure 3: Differences in competitors' colony death rates and effects on plant survival and fecundity can combine to allow wide opportunities for stable coexistence (compare coexistence window size with fig. 2). Fixed rates are $q_2 = 3$, $v_2 = 0.1$, $f_2 = 2.5$, $s_2 = 0.9$, and $v_1 = 0.9$.

on short-term competitive dynamics is relevant to a large literature on virulence evolution, in which analyses involve serial competitive exclusion between disease strains. Much theoretical work invokes trade-offs between disease traits and disease effects on host traits (see, e.g., O'Keefe and Antonovics 2002), though empirical support for such trade-offs is equivocal (Alizon et al. 2009). In addition, potential trade-offs with certain vital rates (notably host recovery, equivalent to our v_x) have been relatively overlooked (e.g., Alizon 2008). Our unconstrained approach emphasizes the importance of all vital rates and also indicates the likely consequences of any given trade-off.

Resource Stage Structure Also Promotes Coexistence

Myrmecophytes are typically long-lived plants, with survival, growth, and reproductive rates that depend on their size (e.g., Heil et al. 1997; Izzo and Vasconcelos 2002; Frederickson and Gordon 2009). Adding demographic structure to the resource population may alter the effects of mutualism, depending on which resource vital rates respond to the competitors. For example, myrmecophyte fecundity not only creates new plant recruits but also shifts

the population stage distribution toward juveniles. Stage-specific survival rates may also shift the stage distribution, and ants may increase myrmecophyte vegetative growth rates, leading to larger ant colonies within affected plants (e.g., Vasconcelos and Davidson 2000). We must incorporate these new effects of resource vital rates on the distribution of resource types as well as the effects of the different resource stages on competitors.

We consider resource stage structure as a dynamic link between distinct resource types. For example, juvenile and adult plants differ demographically but are linked through growth of juveniles, potential regression of adults, and adult reproduction. Before adding these consumer-dependent dynamic links, we first examine how lottery competition works with two independent resource types (e.g., two distinct plant species; fig. 1C). On observing two competitors using two resources in the field, one might assume that they coexist via niche partitioning, or one might invoke results from other models that incorporate multiple resources. Here we show that the presence of multiple resource types increases opportunities for both neutral dynamics and stable coexistence via niche differentiation in lottery competition.

*Two Independent Resources: Niche Partitioning,
Lottery Style*

To allow for two resource types, we let the elements of the population vector \mathbf{n} be the number of individuals of the first resource type occupied by ant 1, the number of the second resource type occupied by ant 1, the first resource occupied by ant 2, and the second resource occupied by ant 2, respectively. Accordingly, q_x and v_x are the queens produced by the two ant species and their vacancy rates on the two resource types. The transition matrix appears in the appendix, and the conditions for neutral dynamics appear in scenario C in table 1. We focus here on the conditions for stable coexistence but note that niche differentiation increases opportunities for neutral dynamics in addition to its recognized stabilizing effect (Hutchinson 1959; MacArthur and Levins 1967; Chesson 1991).

Using our previous methods, we can show that stable coexistence occurs when

$$\frac{v_3}{v_4} > \frac{1}{A} \frac{q_3 v_1 - q_1 v_3}{q_2 v_4 - q_4 v_2} > \frac{v_1}{v_2}, \quad (8)$$

or the same with both inequalities reversed, where the parameter A is the ratio of the abundance of the first resource type to the second. The upper and lower bounds of this expression are equal, preventing stable coexistence, if $v_1/v_2 = v_3/v_4$. Also, the sign of the center term indicates that each ant must have an acquisition-retention advantage at a different plant stage. Unlike mutualism alone, resource structure alone is never destabilizing. Finally, as one resource type becomes more common, the consumer performing better on the rarer resource must have an increasingly large advantage to persist.

Condition (8) implies that niche partitioning in lottery competition entails a difference in consumers' performance on the different plant types. There is no increased tendency for either ant species to colonize individuals of either plant type. Such an additional bias in colonization probability could arise through queen behavior and could contribute to stabilization if the bias were in the same direction as colony performance (Brown 1990). This possibility is an interesting avenue for future research, because empirical work on the relationship between insect host-plant preference and performance has found a wide range of results, from positive to negative associations (e.g., Thompson 1988).

*Dynamically Linked Resource Types:
Yet More Ways to Be a Mutualist*

To add dynamic feedbacks between consumers and their shared resource, we introduce consumer-dependent re-

source vital rates describing transitions between resource stages. Unfortunately, combining plant stage structure and mutualism yields a multidimensionally nonlinear system for which it is difficult to obtain analytical results. Future work will investigate this system using simulations. We can address the core novel issue of competitor influence on the resource stage distribution by examining the simpler system in which the total number of plants is fixed, but individual plants can transition between adults and juveniles via growth (G_x) and regression (R_x ; fig. 1D). The transition matrix and the condition for stable coexistence appear in the appendix, with conditions for neutral dynamics in scenario D in table 1. The coexistence criterion is complex and contains multiple terms, but the terms involving only a single plant transition rate (shown in square brackets in the appendix) dominate the dynamics. The remaining terms describe higher-order effects that are most important when plant transitions are frequent relative to ant colony life span.

The dominant terms in the stable coexistence criterion echo the results of structure alone, with resource population dynamics affecting coexistence in two ways. First, the ratios G_1/R_1 and G_2/R_2 replace the fixed parameter A , since they describe the extent to which each ant species biases the plant demographic structure toward adults. Second, simulations (not shown) demonstrate that coexistence is stabilized if each consumer shifts the resource distribution toward the stage favoring its competitor. Stable coexistence here is similar to the results of De Roos et al. (2008) in that a species can benefit from resource stage structure shifts induced by its competitor, although the mechanism producing the shift differs.

Our analysis suggests that opportunities for coexistence can be broad when competitors interact mutualistically with a stage-structured resource. Stable coexistence results from differences in relative colony death rates (e.g., v_1/v_2) and in overall performance (q/v) between resource life-history stages, especially when combined with a tendency to shift the resource toward a competitor's favored resource stage. Different ant species might perform differently on plants of different stages or sizes for several reasons, including plant patrol or colony defense behaviors or other social behaviors that integrate a colony scattered over many small domatia. Indeed, potential partitioning of resource stages by consumers is observed in nature (Fonseca and Benson 2003). If partitioning by plant size or stage exists, it is also likely that each ant species influences plant structure in favor of its competitor, since herbivore suppression on small plants could result in growth into larger plants, and protection of larger plants could lead to increased reproduction. Finally, ant-mediated differences in plant survival and fecundity could additionally contribute to coexistence, for instance, if the ant species

leading to greater plant fecundity has a lower queen production rate and is also associated with higher plant survival overall.

Conclusion

We have found that consumer-resource mutualisms can promote the stable competitive coexistence of consumers both independently of and in interaction with resource heterogeneity. When a resource population is structured, niche differentiation requires an advantage for one competitor at one stage to be balanced by a disadvantage at the other stage. Whether or not the population is structured, mutualism can stabilize coexistence by widening the range of disadvantage that is compatible with coexistence through indirect negative feedbacks. Resource population structure and mutualism also promote neutral dynamics by providing additional pathways for competitors to affect each other, which can be balanced to achieve fitness equivalence.

Our approach of adding consumer-resource mutualism and resource population structure to an established quantitative model of competition identifies the mechanisms by which these factors, separately and together, can stabilize competitive coexistence. These mechanisms are not specific to a particular biological context or even to our lottery model formulation. For example, our analysis shows that the stabilizing effect of mutualism hinges on resource feedbacks whereby each consumer species indirectly favors its competitor. The biological feature that is necessary for this mechanism to work (in addition to the mutualism) is either some functional differentiation between competitors or partitioning of a heterogeneous resource. Because of the natural history of the ant-plant mutualisms that we use to present these models, we focus on a functional trade-off between plant acquisition and plant retention. In systems in which competitive displacement is more common, a competition-colonization trade-off could work together with consumer-resource feedbacks to stabilize coexistence. In any empirical system, such interaction between multiple potential coexistence mechanisms is an interesting likelihood. In this article, we have demonstrated that the effects of mutualism on resource population structure and niche differentiation can interact. Spatial and temporal heterogeneity are also likely to interact with the mechanisms we have explored here. For instance, in some ant-myrmecophyte systems, local spatial patterns in community structure can affect patterns of queen colonization (Yu and Wilson 2001; Bruna et al. 2005; Izzo et al. 2009).

Application of our models to field systems would involve estimation of competitor and resource vital rates. In many natural systems, measuring the vital rates of not only

competitors but also the resources when controlled by each competitor may be challenging. Our results, however, indicate that to do so is crucial for determining how competitor-mediated resource dynamics affect competitor persistence. In mutualisms without resource structure or in nonmutualistic systems with resource heterogeneity, equations (5) and (8) give conditions for coexistence. In mutualisms that include resource stage structure, if changes in stage structure occur primarily through growth and regression, the dominant terms of equation (A4) (in the appendix) might furnish reasonable predictions. The ant-myrmecophyte mutualisms we use to illustrate these mechanisms are particularly convenient for study of this kind because partners interact in discrete pairs, the mutualisms can be obligate, and all species have limited mobility. For other systems where a guild of mutualists compete for a shared resource population, a serviceable approach may be to parameterize simulations and explore coexistence computationally, keeping in mind the mechanisms we describe here.

In conclusion, mutualism between consumers and their shared resource provides a range of opportunities for the stable coexistence of competitors in the presence or absence of resource population structure and in the absence of other coexistence mechanisms, such as spatial or temporal heterogeneity. However, because mutualism can be stabilizing or destabilizing, its operation should be quantified empirically to determine how frequently mutualism contributes to coexistence in nature. Consumers' effects on resource fecundity, survival, and growth rates have different effects on competitive dynamics. For some natural systems, such as obligate pollination mutualisms (e.g., Addicott 1998; Fleming and Holland 1998; Pellmyr 2003), the mechanism of mutualism may be clear, whereas for others, such as ant-plant protection (e.g., Bronstein 1998; Palmer and Brody 2007) or plant-fungus mutualisms (e.g., Koide et al. 1988; Arnold et al. 2003), it may be less obvious which plant vital rates are affected by mutualist partners. By explicitly modeling the dynamics of competition in the absence and presence of mutualism, we have shown that to identify and quantify these mechanisms is crucial for distinguishing the biologically distinct mechanisms through which mutualism, resource heterogeneity, and both operating together can lead to stable competitive coexistence.

Acknowledgments

We are grateful for financial support from Society in Science: The Branco Weiss Fellowship (C.T.L.) and the National Science Foundation (DEB-0452720 to B.D.I. and DEB-0453631 to E. Bruna). We thank E. Bruna, T. Izzo, F. James, T. E. X. Miller, D. Siegel, B. Spiesman, N. Underwood, and anonymous reviewers for helpful comments

and discussion. This work would not have been possible without the inspiration and background provided by our collaborator H. Vasconcelos.

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Associate Editor: Judith L. Bronstein
Editor: Mark A. McPeck



Left, plant-living ants protect their home from enemies. *Right*, special structures on ant-adapted plants provide homes for ants. Photographs by Brian Inouye.