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Inherent Demographic Stability in Mutualist-Resource-Exploiter Interactions

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ABSTRACT: Core principles of ecological theory predict that, in the absence of other factors, mutualisms should experience destabilizing positive feedback and should be vulnerable to extinction through competitive exclusion by exploiter species. Many effective stabilizing mechanisms address one issue or the other, and many turn upon additional features. Using an explicitly demographic approach, I show that indirect, demography-mediated interactions between mutualists and exploiters can enable mutualist-exploiter coexistence, which in turn can stabilize the abundances of mutualists, exploiters, and their shared resources. This occurs because of the distinct resource demographic responses that are inherent to interaction with mutualistic and exploitative partners and can occur in long-lasting, exclusive interactions, such as protection mutualisms, as well as in apparently very different, short-lived mutualistic interactions, such as pollination. The key necessary factor—demographic response to interspecific interaction—is common in nature. Some demographic structure is also necessary and is generated through interspecific interaction in long-lasting associations; it is also very common in natural populations. Thus, the explicitly demographic and multispecies approach taken here constitutes a potentially promising single explanation for the apparent stability of mutualism in a wide range of natural systems.

Keywords: mutualism, exploitation, coexistence, consumer-dependent demography, lottery competition, consumer-resource dynamics.

Introduction

Mutually beneficial interactions are widespread and important in nature. Established principles of ecological theory for species pairs indicate that mutualism presents two distinct dynamical issues. First, mutualism is defined by reciprocal benefit: one species benefits another, which in turn benefits the first. This reciprocal benefit constitutes a positive feedback loop, and positive feedbacks are destabilizing (e.g., May 1973). The second issue is susceptibility to extinction via exploitation (Bronstein 2001). Although much work on this problem has been evolutionary, fo-

cused on the long-run erosion of mutualistic partnership, the shorter-term ecological issue of competitive exclusion plays a key role (e.g., Yu 2001; Ferrière et al. 2002). The greater the benefit a mutualist provides its partner, the higher a cost it is presumed to pay in its own fitness and the more vulnerable it should therefore be to invasion by another species, which can extract benefits while paying lower costs. A hallowed principle of ecology holds that a single resource or host species can support only a single consumer (e.g., Levin 1970), so invasion by a competitively superior exploiter species should lead to extinction of the mutualist. Thus, strong theoretical principles support conceptualization of mutualism as dynamically unruly if not fundamentally unstable.

Many mechanisms have been demonstrated to stabilize mutualism in either sense, although usually not both simultaneously. Addressing positive feedback conventionally equates with achieving a stable two-species equilibrium. Standard forms of density-dependent mortality are alone insufficient to check population growth in the presence of mutualism, so researchers add a function describing mutualistic benefit that attenuates in partner abundance (Holland 2012; Johnson and Amarasekare 2013). Such cross-species density dependence in the interaction between mutualists is biologically reasonable and reduces positive feedback at high densities, but it does not alone restrain population growth. Work addressing mutualism's apparent vulnerability to a competitively superior exploiter focuses on counteracting the mutualist's putative competitive inferiority (reviewed in Jones et al. 2012). Currently prominent is work on sanctions or other forms of choice, whereby a host can penalize exploiters and/or favor more mutualistic partners (e.g., Kiers et al. 2003; Frederickson 2013); other work includes extrinsic competitive asymmetry, such that a mutualist is actually competitively superior to an exploiter (e.g., Morris et al. 2003; Holland et al. 2013). (Factors that favor mutualists can shift the competitive question to what maintains exploiters in the system.) General mechanisms for maintaining a diversity of

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competing consumers can apply (Palmer et al. 2003), including strong density dependence in superior competitors (e.g., Morris et al. 2003; McPeck 2012) and temporal or spatial heterogeneity (e.g., Yu and Wilson 2001; Wilson et al. 2003; Yamamura et al. 2004). All these mechanisms effectively protect mutualism, but from the outset they invoke external or additional features of the interaction. This does not detract from their applicability, but it is a difference from the work presented here, which builds from the demographic expression of mutualism itself, its difference from exploitation, and the dynamic consequences of the two.

Here I show that demography can mediate indirect interactions between mutualists and exploiters and that these interactions can stabilize mutualist-resource-exploiter community modules. This provides a single, synthetic potential explanation for the apparent stability of mutualism in nature. The key process is consumer-dependent resource demography, which expresses the distinct effects of each consumer on the host or resource-producing species explicitly in terms of the survival and fecundity of the host or resource species. Because of the resulting demographic dynamics, mutualists can be vulnerable to invasion by exploiters yet resistant to subsequent competitive exclusion. Mutualist-exploiter coexistence can stabilize the abundances of both consumers and their host, if not in the usual sense of producing a stable equilibrium point. This suggests a shift in perspective away from a feedback-driven system restrained and protected by additional factors, toward a concept of mutualism as producing much more moderately growing multispecies systems more weakly or infrequently encountering external restraint. In short, spelling out the demography shows that mutualism may frequently be more well behaved than we have previously had reason to believe, even in the absence of other factors. The critical role played by the exploiter also urges consideration of mutualism as a property of a community rather than of a species pair as well as broadening consideration of interacting modules beyond narrow feeding guilds.

In this article, an exploiter is a species that meets the criteria of the problem of exploitation as originally stated. An exploiter must consume resources in the same way as the mutualistic consumer from a dynamic standpoint, so that the two are resource competitors. Furthermore, relative to the mutualist, an exploiter must harm the host or resource species and itself benefit as a result, such that it can indeed naively be expected to be the superior competitor. Except in the case of by-product mutualisms, it seems reasonable that in providing mutualistic benefit, a mutualist frequently must sacrifice some of its own performance, therefore becoming vulnerable to competition. A more restrictive definition of exploitation—requiring, for example, that consumers inflict a net fitness cost on the

resource species—would not change the dynamics described here because all results are consistent with absolute as well as relative harm to the resource species.

In the next two sections, I present explicitly demographic models for two cases that differ dramatically in the duration, scale, and intensity of the interaction between a host and its consumers. The cases lie on opposite ends of a continuum describing the length of time during which interaction is exclusive, and the contrast between them highlights the shared demographic features that can be powerfully stabilizing in otherwise disparate natural systems. There is no density dependence: the host is limited only by consumption, and the two consumers are limited only by the abundance of their shared resource. In both cases, the host, the mutualist, and the exploiter can coexist at stable abundances via demography-mediated interactions.

Long-Lasting, One-at-a-Time, Obligate Interactions

Some mutualists form long-lasting associations, also known as symbioses (Douglas 2010). Examples include residential protection mutualisms, such as between anemones and anemonefish (Fautin 1991) or between plant-nesting ants and their specialized host plants (Heil and McKey 2003). As an exemplar of this type of interaction, I consider cases where, on the temporal scale of meaningful changes in host demography, only one consumer species (and, usually, only one consumer individual or colony) interacts with a host individual at a given time. When such long-lived, one-at-a-time interactions are obligate, such as when ant colonies can establish nests nowhere else than in host plants, and when hosts are the limiting resource, then consumer species compete for access to hosts. But competing consumers do not (or only subsidiarily) consume host tissues; instead, they temporarily consume space by making host individuals unavailable to competitors.

When consumers cannot be competitively displaced once established, then the most appropriate model to describe their competition for renewable space is the lottery model (Sale 1977; Yu and Wilson 2001). Lottery competition does not admit stable coexistence of two or more competitors (Chesson and Warner 1981). In long-lasting mutualisms, however, individual hosts are not passive units of space but living entities whose survival and reproduction respond to association with consumer species. Here I use the model developed for these dynamics by Lee and Inouye (2010), without the additional density dependence imposed on the host in that article: the only two elements of the model are lottery competition for a living resource and distinct responses of resource survival and fecundity to different consumers.

Because host demographic rates depend on which consumer is present, consumer identity structures the host

population. The matrix equation $\mathbf{n}(t + 1) = \mathbf{M}(t)\mathbf{n}(t)$ captures the dynamics of all species, where $\mathbf{n}(t)$ is a vector describing the abundance of hosts associating with each consumer at time interval t and $\mathbf{M}(t)$ is a matrix describing host transitions between consumers at time t . Additional equations to describe consumer abundance are not needed because consumers' association with hosts is obligate. To focus on mutualist-exploiter competition, I assume for the following analysis that all hosts associate with one of two consumers by the end of each model time interval. This is reasonable once host abundance becomes limiting to both consumers.

Consumers form associations with available hosts via searching recruits, which are born at the per capita rate b_m for mutualists and b_e for another species, which will be restricted below to an exploiter. The lottery-model probability that the mutualist occupies an available host, $P(t)$, is equal to the fraction of mutualists among searching recruits (see, e.g., Chesson and Warner 1981):

$$P(t) = \frac{b_m n_m(t)}{b_m n_m(t) + b_e n_e(t)}. \tag{1}$$

Hosts survive and reproduce at consumer-dependent rates S_m or S_e and F_m or F_e , respectively. Surviving hosts become available for association when the resident consumer vacates, which occurs at rate v_m or v_e through mortality; new host recruits are available immediately. Then the transition matrix is

$$\mathbf{M}(t) = \begin{bmatrix} F_m P(t) + S_m(1 - v_m + v_m P(t)) & (F_e + S_e v_e)P(t) \\ (F_m + S_m v_m)(1 - P(t)) & F_e(1 - P(t)) + S_e(1 - v_e P(t)) \end{bmatrix}, \tag{2}$$

where the first column describes transitions from association with the mutualist to association with the mutualist and the other consumer, respectively, and the second column describes transitions from association with the other consumer (Lee and Inouye 2010).

Due to the dependence of $P(t)$ on $\mathbf{n}(t)$, this model is nonlinear, but it reaches a linear-like equilibrium where it is characterized by the eigenvalue equation, $\bar{\lambda}\bar{\mathbf{u}} = \bar{\mathbf{M}}\bar{\mathbf{u}}$ (see, e.g., Caswell 2001 for the role played by the eigenvalue equation in linear models). Here, the overbars denote equilibrium, and the population achieves an asymptotic growth rate $\bar{\lambda}$ and equilibrium relative abundances of the different consumers (and host associations) $\bar{\mathbf{u}} = (\bar{u}_m \bar{u}_e)^T$, where the superscript T denotes a transpose. Such linear-like equilibrium occurs in other, structurally similar nonlinear demographic models (e.g., Caswell 2008; Lee and Tuljapurkar 2008). It indicates that, just as in familiar linear demographic models, the equilibrium relative abundances of consumer associations (or, in other words, the equilibrium

structure) is a key feature of equilibrium. Here I use the equilibrium structure vector $\bar{\mathbf{u}}$ to determine conditions for coexistence of the two consumers. One can find the equilibrium structure vector using methods summarized in the appendix (available online). When both consumers have positive and finite abundance at equilibrium, the consumers coexist; the criterion for this is

$$\frac{F_m + S_m v_m}{S_m - S_e + F_m + S_e v_e} > \frac{b_m}{b_e} > \frac{S_e - S_m + F_e + S_m v_m}{F_e + S_e v_e}, \tag{3}$$

or the same condition with both inequalities reversed (see the appendix for more details).

Interpretation of the coexistence criterion can be complex (Lee and Inouye 2010), but stable coexistence is most likely and most clear-cut when one consumer emphasizes continuation of existing mutualistic partnerships through its own survival and through promotion of host performance, while the other emphasizes acquisition of available hosts through a high birth rate at the expense of host survival and fecundity. This second consumer meets the definition of an exploiter. Coexistence can result because this trade-off with host demography creates a distinction between acquisition and retention of hosts that does not exist in the basic lottery model, providing a pathway for indirect interaction through which each competitor can favor the other. For instance, when a mutualist promotes host fecundity, it indirectly favors an acquisition-focused competitor, which needs new host recruits because the mutualist better retains existing ones (Lee and Inouye 2010). When the exploiter becomes abundant, it suppresses host fecundity, reducing the supply of new host recruits on which it particularly depends. If the exploiter does not protect the survival of its own hosts, it additionally harms itself but not the mutualist, favoring its retention-focused competitor in a way not possible in standard consumer-resource approaches.

As a result of these dynamics, even very harmful exploiters can fail to exclude even very beneficial mutualists. Indeed, the greater the difference between consumers in their effects on the host, the greater the possibility that an exploiter with a substantial advantage in reproductive output ($b_e > b_m$), although easily able to invade the mutualism, is nonetheless incapable of excluding its competitor due to the poor performance of its associated hosts. Figures 1 and 2 illustrate the range in the exploiter's reproductive advantage that is consistent with competitive coexistence. At the left side of figure 1, the consumers have the same effect on host survival and fecundity; stable coexistence is impossible, although neutral coexistence occurs if $b_e = b_m$. But with an exploiter that is increasingly less beneficial to host survival, coexistence occurs for larger ranges of exploiter reproductive rates, all of which are

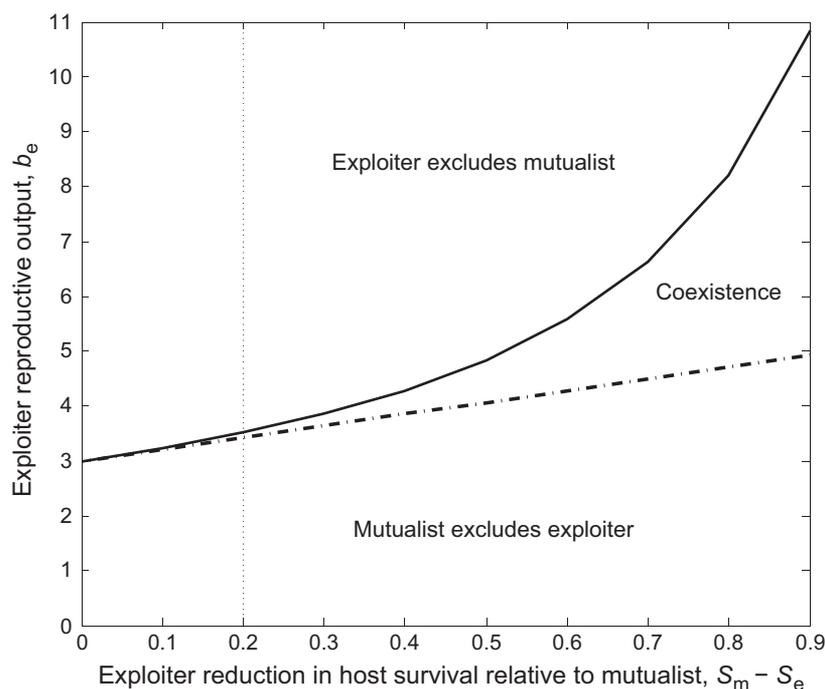


Figure 1: A mutualist can be vulnerable to invasion by an exploiter yet resist subsequent competitive exclusion. Broken and solid lines show the levels of exploiter reproductive output (b_e) necessary for the exploiter to invade and persist and to exclude the mutualist, respectively. With the mutualist, host survival is $S_m = 0.95$, and fecundity is $F_m = 1.05$. The X-axis shows the difference in host survival due to the exploiter, $S_m - S_e$. Mutualist mortality and reproduction are $\nu_m = 0.15$ and $b_m = 3$; the exploiter's mortality rate and effect on host fecundity are set equal to the mutualist's, for simplicity.

greater—and some of which are very substantially greater—than the mutualist's. This is despite the fact that greater reproductive output is required for the exploiter to invade (broken line) to compensate for its hosts' lower survival.

Figure 2 illustrates additional effects of differences between consumers in host fecundity. Effects on host survival (fig. 1) and effects on host fecundity (fig. 2) could serve as the independent axes of a combined three-dimensional figure, but because the purpose of the figures is to illustrate the potential for each factor to promote coexistence (and for visual clarity), figure 2 is a cross section through this three-dimensional space; it intersects figure 1 at right angles at the vertical dotted line in figure 1. As does figure 1, figure 2 shows that increasing differences between the exploiter and the mutualist in their effects on the host increases the likelihood of coexistence. Both figures also include cases where such extreme dichotomy between mutualist and exploiter, as described above, is not strictly necessary.

Because of the one-to-one nature of interactions, the model implicitly includes mutualistic benefits to the host that attenuate in the density of the mutualistic consumer. But there is no density dependence, and although the two consumers coexist at stable relative abundances, all three species' absolute abundances can eventually grow expo-

nentially (fig. 3A). Stably coexisting consumers, however, exert a combined influence on host population growth, so that the same dynamic feedbacks that stabilize the relative abundances of the two consumers can also alone stabilize the absolute abundances of all three species (fig. 3B).

To determine criteria for mutual coregulation of host and consumer densities, note that the equilibrium growth rate $\bar{\lambda}$ of hosts (and, therefore, of the three-species system) is a weighted average of growth rates given each consumer alone:

$$\bar{\lambda} = \frac{1}{1 + \bar{u}_e} (S_m + F_m) + \frac{\bar{u}_e}{1 + \bar{u}_e} (S_e + F_e). \quad (4)$$

Here, the equilibrium abundance of hosts in association with mutualists is scaled to 1, so that \bar{u}_e is the equilibrium relative abundance of hosts associating with exploiters and total abundance is proportional to $1 + \bar{u}_e$. The first term in this expression describes the proportion of hosts associating with mutualists, and the second describes the proportion associating with exploiters, with terms in parentheses describing the per capita contribution of each type of host to the next generation.

Now let $\bar{\lambda} = 1$ and rearrange equation (4) into an expression for \bar{u}_e . Then using $\bar{\mathbf{u}} = (1 \ \bar{u}_e)^T$ and $\bar{\lambda} = 1$ in the

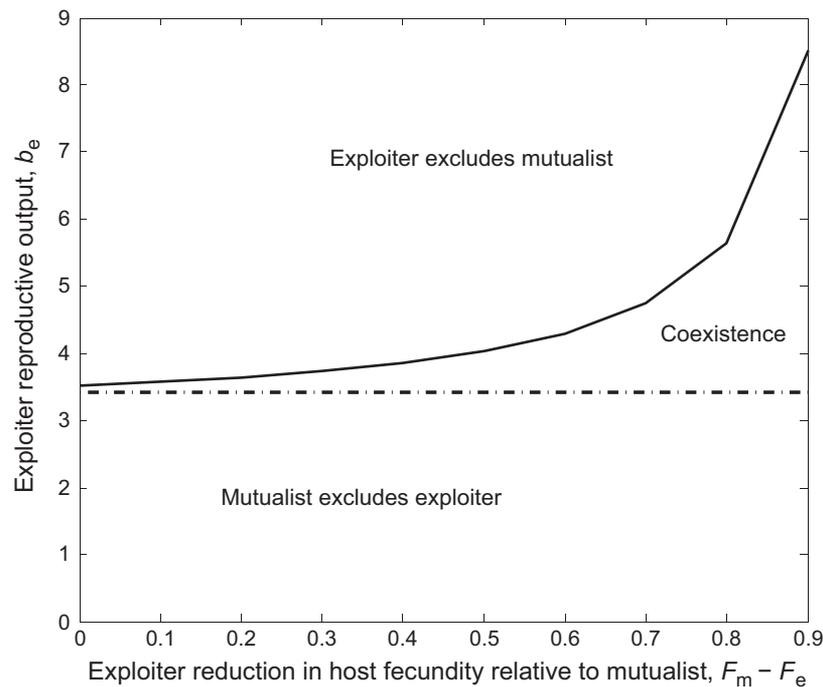


Figure 2: Differences between consumers in their effects on host fecundity also promote coexistence. Differences in survival are held constant: with all other parameters as in figure 1, host survival with the exploiter is $S_e = 0.75$ (shown by the vertical dotted line in fig. 1). The X-axis shows the difference in host fecundity due to the exploiter, $F_m - F_e$; the Y-axis is as in figure 1. At the left side of the figure, competitors' effects on host fecundity are equal, and opportunities for coexistence are slim. Greater reductions in host fecundity due to the exploiter increase the likelihood of mutualist-exploiter coexistence.

equilibrium eigenvalue equation to constrain the equilibrium matrix \bar{M} , it is a matter of algebra to show that stasis of abundances occurs when the host population grows with the mutualistic consumer alone ($\lambda_m = S_m + F_m > 1$) and declines with the exploiter alone ($\lambda_e = S_e + F_e < 1$) as well as when

$$\frac{b_m}{1 - S_m(1 - v_m)} = \frac{b_e}{1 - S_e(1 - v_e)}. \quad (5)$$

Criterion (5) expresses a trade-off between consumer reproduction and continuation of established consumer-host relationships: the denominator on either side of equation (5) is the sum of the rates at which partners can dissociate (as the association continues only if the host individual and the consumer both survive). Similarity of the two sides of the criterion is likely when consumer reproduction occurs at the expense of continued association and vice versa, and the equilibrium is stable when the mutualist is more likely to continue established partnerships and the exploiter to terminate them through departure or through less effective protection of host survival ($1 - S_m(1 - v_m) < 1 - S_e(1 - v_e)$). Both are in accord with intuitive expectations regarding mutualism and exploita-

tion. Thus, the distinction between the two types of consumers favors stabilization of abundances, just as it does coexistence.

It is tempting here to conclude that if the mutualist is good for the host and the exploiter bad, their effects on the host simply balance, but this is not the case. If it were, the eventual system growth rate would be neutrally stable: starting from equilibrium, an increase in the number of mutualists would outweigh the exploiter, so to speak, causing growth in all three populations. Here, demographic feedbacks between consumers and host stabilize the growth rate. An increase in either consumer from equilibrium indirectly favors its competitor, as previously described, so that no effect on the growth rate results. Furthermore, slight deviation from balance between the traits of the two consumers (eq. [5]) does not result in competitive exclusion, as in the base lottery model (Chesson and Warner 1981). Instead, provided the coexistence criteria are still met, shifting the consumers' traits away from precise balance shifts the equilibrium relative abundances of the consumers; this (not transient changes in abundance) shifts the stable host population growth rate in the direction of the consumer with the trait advantage. Slight growth occurs if the mutualist has the advantage, and slight decline occurs if the

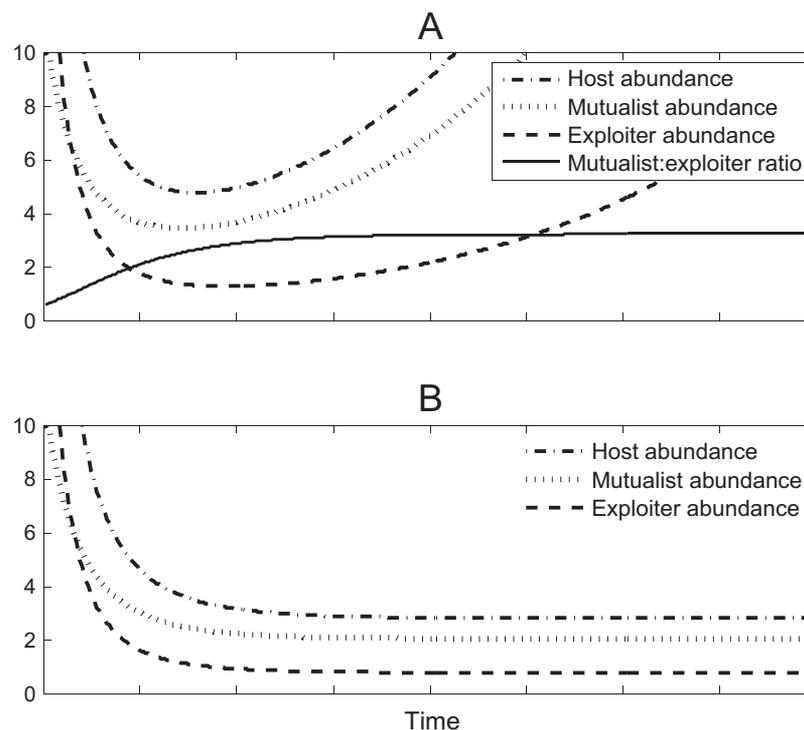


Figure 3: Consumer-dependent host demography can enable stabilization of all species' abundances in addition to mutualist-exploiter coexistence. *A*, Mutualist-exploiter coexistence alone means that the mutualist and the exploiter reach a stable relative abundance, but in general the absolute abundances of all species continue to change. *B*, Mutual stabilization of host, mutualist, and exploiter abundances can occur in the absence of external stabilizing factors when $b_e = b_m[1 - S_e(1 - v_e)]/[1 - S_m(1 - v_m)] = 5.6$ (see eq. [5]). In panel *A*, $b_e = 5.5$. Other parameters are as in figure 1, and $S_e = 0.75$ as in figure 2. Simulation code appears in the appendix (available online).

exploiter has it. This is because the direct advantage to one consumer in its reproduction : retention ratio is counteracted by indirect advantage to the other via the dynamics of the host population.

Complete stasis of population abundances requires precise equality in coregulation criterion (5), and it is therefore unlikely. But a coexisting exploiter always reduces the population growth of mutualists, and the multispecies interaction leads to moderate population change (growth rate near 1) whenever the two sides of equation (5) are similar. As we have seen, similarity of the two sides should frequently occur, given intuitive expectations regarding trade-offs in the life history and behavior of mutualists and exploiters. As a result, I argue for an idea of mutualism as a reasonably subdued multispecies system, albeit one not necessarily constrained to particular steady state abundances. Especially in the presence of environmental variation, which also tends to reduce long-run population growth (Lewontin and Cohen 1969), modest population change could be very difficult to distinguish from fluctuation around an equilibrium. Supposing limitation of positive growth to be due ultimately to some extrinsic factor,

the burden on that factor to restrain population growth would be greatly reduced, and detection of that factor in the field would be correspondingly more challenging. Thus, further empirical work to quantify differences between consumers in their effects on host demography (e.g., Bruna et al. 2004, 2014; Frederickson 2005; Miller 2007; Young et al. 2008; Palmer et al. 2010) could be fruitful to determine any role played by consumer-dependent demography in maintaining apparently stable, long-lasting, one-at-a-time mutualisms in nature. The next section shows that the same mechanisms can similarly stabilize mutualisms at the other extreme of temporal scale: mutualisms with interactions that are very short in duration and where multiple consumers can interact with a host simultaneously.

Short-Lived, Potentially Simultaneous Interactions

In many mutualisms, several species can interact with a host individual during a demographically meaningful interval. This is most likely when interaction is short-lived, in contrast with the lottery case of the previous section. Pollination

is an excellent example: interaction between plant hosts and animal visitors is momentary, multiple visits are likely during a flowering season, and, from the point of view of host demography, multiple visits are effectively simultaneous. Simultaneous interaction can also occur in long-lasting symbioses, such as rhizobial (e.g., Denison 2000) and mycorrhizal (e.g., Allen et al. 2003) associations, but because of its visibility and familiarity—and the relatively straightforward mechanism of host demographic response to interaction—pollination is the example that guides the language of this section.

A host species that interacts simultaneously with multiple species is a resource that is available to multiple consumers (Holland and DeAngelis 2010), especially given that the host species frequently provides a reward of food resources, such as nectar. An appropriate modeling starting point is a system of consumer-resource equations (e.g., MacArthur 1972; Tilman 1982). The mutualism need not be obligate as long as the same species (or the resources produced by it) is the limiting resource for all consumers in the model. Much previous work with consumer-resource models demonstrates that the number of coexisting consumers cannot exceed the number of limiting resources (e.g., Levin 1970). Therefore, given a single resource species, a mutualist and an exploiter cannot coexist in the absence of additional stabilizing factors.

Distinct demographic responses of the resource species to different consumer species, such as are characteristic of mutualism and exploitation, can alone enable coexistence, provided that the resource species is structured by age, size, or developmental stage (Lee et al. 2011). This echoes the result of the previous section, except that additional demographic structure in the resource species is necessary here because the short duration of interactions prevents association with consumers from itself structuring the resource species. Demographic structure, however, is common in nature, and the implications of consumer-dependent resource demography for the stability of mutualism are the same as in long-lived, one-at-a-time associations.

To describe consumer-resource interactions with demographic structure in the resource species, I use the model developed in Lee et al. (2011), leaving out the external density dependence there imposed on the resource. The resource species is limited only by consumption, and consumers are limited only by available resources. As before, I begin with a matrix equation for the demography of the resource species, $\mathbf{r}(t + 1) = \mathbf{A}(t)\mathbf{r}(t)$. The vector $\mathbf{r}(t) = \{r_j(t)\}$ describes the abundance of each age, size, or stage class of the resource species at time interval t . The matrix $\mathbf{A}(t)$ describes demographic transitions of the resource species at time t , and its elements depend on the consumers.

The abundance of the i th consumer is determined by

$$C_i(t + 1) = \sum_j \mu_{ij}(t)\beta_{ij}r_j(t), \tag{6}$$

where β_{ij} converts units of the j th stage of the resource species into units of consumer i and μ_{ij} describes resource use or uptake:

$$\mu_{ij}(t) = \begin{cases} c_{ij}C_i(t) & \text{if } r_j(t) \geq \sum_i c_{ij}C_i(t)r_j(t), \\ \frac{c_{ij}C_i(t)}{\sum_i c_{ij}C_i(t)} & \text{if } r_j(t) < \sum_i c_{ij}C_i(t)r_j(t). \end{cases} \tag{7}$$

Here, following established work (e.g., MacArthur 1972; Tilman 1982), the resource utilization function c_{ij} is a per capita, per-unit resource use or uptake rate. The first case in equation (7) parallels the previous work; the second case merely prevents resource use from exceeding the finite resources available during each unit of discrete time and states that the realized resource use is a linear function of the proportion of a single species' ideal use among the total ideal use. This simple functional form and its assumptions also parallel the development of $P(t)$ in the lottery model described above (see the appendix for additional explanation of resource use and consumer dynamics).

For each stage of the resource species, demographic transitions take place according to a weighted average across consumers of transition rates given each consumer alone, with μ_{ij} providing the weights. Thus, each consumer's demographic effect is proportional to its realized resource use, and the effects of multiple consumers combine linearly. These assumptions are intended as a simplest starting point (see Lee et al. 2011 for a more detailed discussion). To focus on resource competition and to simplify presentation and analysis, I here assume that consumer populations have become limited by resources and that $\sum_i \mu_{ij} = 1$ for each j in each time interval. Then, given a simple example resource species life history with potentially persistent adult and juvenile developmental stages but where only adults reproduce, the transition matrix is

$$\mathbf{A}(t) = \begin{bmatrix} \sum_i \mu_{ij}(t)s_{ij}(1 - g_i) & \sum_i \mu_{iA}(t)f_i \\ \sum_i \mu_{ij}(t)s_{ij}g_i & \sum_i \mu_{iA}(t)s_{iA} \end{bmatrix}. \tag{8}$$

Here, s_{ij} indicates the survival rate of juveniles when the i th consumer uses all of the juvenile resources. Similarly, g_i is the growth rate of juveniles to adults (conditional on survival), and s_{iA} and f_i are adult survival and reproduction, all given the i th consumer. The appendix gives more information on the interpretation of the matrix elements. Through μ_{ij} , the matrix elements depend on the consumers, which in turn depend on resources. Nonlinearity in the matrix model thus captures the coupling between consumer

and resource populations. As before, this nonlinear model reaches a linear-like equilibrium, where consumer relative abundance stabilizes, matrix elements cease to change, and the system eventually achieves an equilibrium growth rate, $\bar{\lambda}$.

Using two consumers and two stages in the resource species, Lee et al. (2011) show that consumer-dependent resource demography can generate key qualitative differences from established consumer-resource expectations. First, stable coexistence of two consumers is possible given a single, structured resource species even if both consumers use resources identically ($\mathbf{c}_1 = \{c_{ij}\} \propto \mathbf{c}_2$), provided the appropriate unique effects of each competitor on the demography of the resource species. Second, although coexistence is easiest if consumers each specialize on a unique resource stage, it is not assured; this is due to the demographic interdependence of resource stages. The first result means that consumer-dependent resource demography can promote mutualist-exploiter coexistence despite substantial overlap in use of stage classes of the resource species. The second means that even complete resource-stage specialization does not eliminate resource competition between consumers. Quantitative details of coexistence criteria and the strength of competition depend on the life-history details of the resource species (Lee et al. 2011), and the simple, general life history used here is meant to be merely illustrative, not representative. Therefore, here I focus not on coexistence but on possibilities for multispecies stabilization of abundances. To do this, I use the case where consumers specialize on different stages of the resource species, as this makes coexistence easy and simplifies the otherwise complex analysis. But I reiterate that complete specialization is not necessary for consumers to coexist, and it does not eliminate competition between consumers.

Consider, then, a mutualist that specializes on the reproductive stage of the resource species, as a pollinator would on the flowering stage of a plant, and a consumer that specializes on juveniles. Here, resource structure can be more subtle than the juvenile/adult terminology implies: for instance, a florivore that consumes flowers before they can be pollinated (e.g., Bronstein et al. 2003) would be consistent with the demography of a juvenile-specialist consumer. The juvenile consumer satisfies the definition of an exploiter if it experiences some benefit (expressed via, say, resource conversion efficiency, β) in association with a detriment to resource demography. Using the methods described above (see the appendix for details), it is possible to show that the mutualist, resource, and exploiter populations are stationary at steady state ($\bar{\lambda} = 1$) if the resource population grows given the mutualist alone and declines given the exploiter alone, if the two consumers coexist and if

$$\frac{g_{eje}}{1 - s_{je}} = \frac{1 - s_{Am}}{f_m - (1 - s_{Am})}. \quad (9)$$

Thus, multispecies stabilization of abundances is possible in mutualisms where interactions are short-lived. Figure 4 shows that the multispecies interaction can stabilize not only the positive feedback between the resource species and its mutualist but also the negative feedback responsible for resource-exploiter oscillation.

In equation (9), greater fecundity or lower adult mortality of the resource species in the presence of the mutualist would make the right-hand side smaller, and lower juvenile growth or higher juvenile mortality with the exploiter would be needed on the left-hand side. Thus, similarity between the mutualist and the exploiter in the magnitude of their opposite effects on the resource species can moderate resource population change. As before, precise stasis of species' abundances is not as important as the mechanisms by which consumer-dependent demography of the resource species can stabilize the dynamics of multiple interacting species. Increases in the mutualist population increase the resource species' fecundity, increasing the relative frequency of resource juveniles and thereby favoring the exploiter. Conversely, increases in the exploiter population shift the resource structure in favor of the mutualist, through low survival of juveniles in figure 4. Even if abundances continue to change, the dynamics of the multispecies system are subdued relative to the dynamics of species pairs, reducing the appearance of instability as well as the burden on any external factors to provide restraint. I briefly discuss the contrast between these dynamics and those of another recent study of resource-mutualist-exploiter dynamics (Holland et al. 2013) in the appendix.

Stage structure in the resource species and species-specific demographic responses are the critical elements of these results, and they are common in natural populations; consumer specialization on different resource stages is not required and is included here for simplicity. Structure in the resource species can be defined in part by consumers' resource use. The florivore example given above illustrates one such case and also demonstrates how exploiters as defined here can compete with mutualists despite occupying a different feeding guild. Consumers can attack a distinct resource stage even when they are members of a pollinator's guild, such as when nonpollinating parasites attack ovules fertilized by a pollinating seed predator (Morris et al. 2003). As another example, if pollinators avoid previously pollinated flowers and nectar robbers do not (Holland et al. 2013), then one could consider unpollinated flowers and pollinated ones to be distinct demographic classes, only the first of which is used by pollinators but both of which are used by nectar robbers. This work urges careful consideration of whether demographic structure is present and in what ways different consumers use resource stages. It could help to identify previously unrecognized structure in the resource species as well as to identify exploiters using

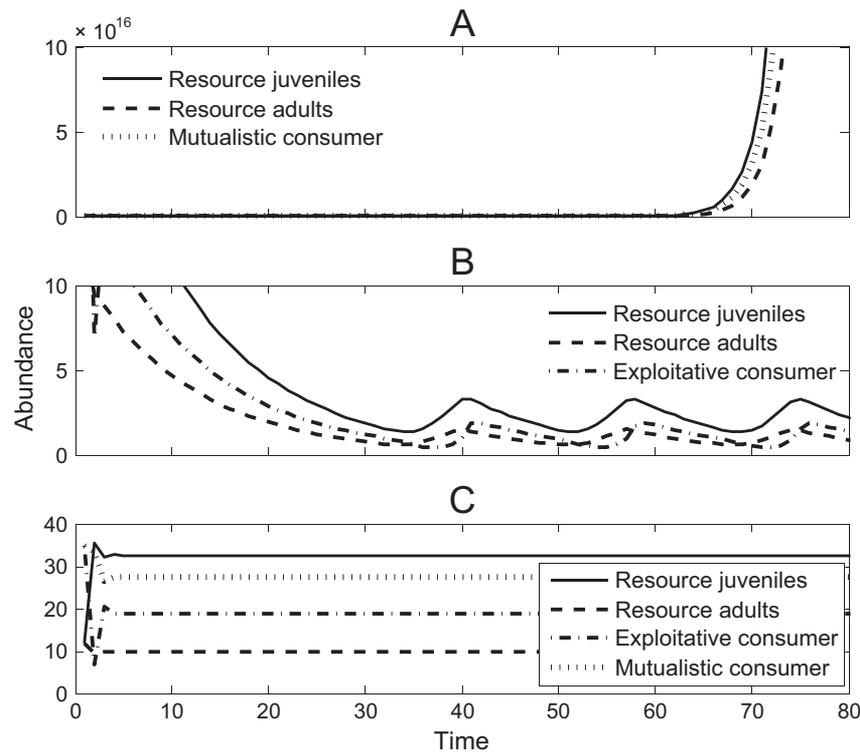


Figure 4: Mutualist-resource-exploiter interaction alone can stabilize all species' abundances when interactions are short-lived. *A*, Mutualist and resource alone generate positive feedback, leading to unrestrained growth. *B*, Consumer and resource alone generate negative feedback, leading to cycles. *C*, The three species together mutually stabilize their own abundances. Demographic parameters represent a perennial plant with a juvenile stage exploited by an herbivore and an adult stage visited by a pollinator. Plant fecundity and adult survival with the mutualist are $f_m = 2.8$ and $s_{Am} = 0.7$, respectively. With the exploiter, juvenile survival $s_{je} = 0.25$, and growth to the adult stage $g_e = 1 + (1/s_{je})[f_m(s_{je} - 1)/(1 - s_{Am} - f_m) - 1] = 0.36$ (see text). Without the exploiter, juvenile survival $s_j = 0.9$, and growth $g = 0.45$. Without the mutualist, $f = 1.8$, and adult survival is $s_A = 0.7$ (pollinators do not affect survival). Further explanation and code for this simulation appear in the appendix (available online).

very different feeding strategies, such as herbivores of seedlings or juvenile plants. Indeed, given the ubiquity of both herbivory and plant stage structure, conceptualizing herbivores and other consumers as exploiters of mutualisms when appropriate could be very helpful for understanding the dynamics of a mutualistic interaction in hand. When mutualists and exploiters do use resource stages similarly, as is frequently the case, it would be helpful to assess resource use and consumer-dependent resource demography quantitatively in the field and to use the data to parameterize a specific model (see the appendix for example computer code¹) to determine any role of the dynamics described here.

Pollinators and herbivores can be highly specialized or nonspecialized. The model here does not address consumer use of many resource species, unless a single resource limits all consumers. The key concepts apply, however, at higher

levels of organization. If a pollinator benefits many plant species and benefits from all, then the suite of plants and their pollinator should experience positive feedback, just as would a mutualistic pair. If consumer-dependent resource demography prevents herbivore exploiters from driving the pollinators' resources too low, then the entire multispecies, mixed-guild community could experience some stabilization as a result. Overall, this work suggests that a broadening of perspective on species interactions beyond narrowly defined guilds could help to articulate important questions about population and community dynamics.

Conclusion

The work described here elucidates how consumer-dependent demography can stabilize mutualist, resource, and exploiter populations, promoting coexistence and greatly moderating population dynamics. This represents a synthetic potential solution to the problems of the population dynamics of mutualism and complements other findings

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

on the ecological and evolutionary importance of diversity in systems containing mutualisms (Foster and Kokko 2006; Palmer et al. 2010; Afkhami et al. 2014).

The definition of exploitation in this article centers around competition for a shared resource. This focus on population interaction contrasts with other definitions, which commonly and reasonably focus on fitness differences (e.g., Bronstein 2001; Frederickson 2013). Here, even substantial fitness differences can be insufficient to constitute competitive threat (e.g., figs. 1, 2), identifying this weakness in the standard statement of the problem of exploitation. How important is a fitness difference if competitive superiority does not necessarily follow? As an addition to fitness, therefore, this work highlights resource consumption, an important feature of mutualism (Holland and DeAngelis 2010) that here can open the idea of exploitation to other feeding guilds, depending on what resource is consumed and how. An herbivore of an ant plant is generally not a competitor with a plant ant, as the ant temporarily consumes nesting space, but an herbivore can compete with a pollinator, as both permanently consume plant biomass. These considerations could help to identify previously unrecognized exploitation of mutualism.

As mentioned above, although precise stasis of population abundances via the processes described here is unlikely, moderation of mutualism-driven growth is assured by a coexisting exploiter. In addition, I argue that growth rates near 1 are likely in long-lasting interactions, and I give criteria for near stasis in the case of short-lived interactions. Most importantly, the results of this work support an idea of mutualism as a reasonably subdued multispecies system that is stabilized, if not stationary, as a result of the demography of mutualism and exploitation.

The key to the dual stability of the multispecies dynamics described here is distinct responses of the demography of the host or resource species to association with different consumers, such as are implicit in any distinction between mutualists and exploiters. These provide pathways of indirect interaction through which mutualism's very vulnerability to exploitation can result in its stabilization. Because the dynamics of the multispecies community module are not necessarily predictable from the dynamics of component pairwise interactions, study of species assemblages or whole communities may prove to be a fruitful complement to study focused on the mutualistic interaction itself.

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