Eco-Evolutionary Dynamics of Mutualists and Exploiters

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ABSTRACT: With the growing recognition of exploiters as a prominent and enduring feature of many mutualisms, there is a need to understand the ecological and evolutionary dynamics of mutualisms in the context of exploitation. Here, we model coevolution between mutualist and exploiter birth rates, using an obligate pollinating seed parasite mutualism associated with a nonpollinating exploiter as a reference system. In this system, mutualist and exploiter larvae parasitize the host plant, competing for and consuming seeds. Evolution of the mutualist determines which exploiters can invade successfully. Subsequent coevolution with an exploiter has a strong, predictable influence on mutualist-exploiter coexistence, mutualist and exploiter phenotypes, and species abundances. Weak mutualist competition promotes “evolutionary purging” of the exploiter, while weak exploiter competition leads to “evolutionary suicide” of the system. When stable, long-term coexistence occurs, we identify two main “trait-abundance syndromes” that have three novel implications. (1) Persistent, highly parasitic exploiters can be favored by coevolution. (2) Even then, the density of coevolved mutualists can be high. (3) Low plant density results primarily from the evolution of mutualist, not exploiter, birth rate and density. To evaluate these predictions, studies are needed that identify and compare populations with and without exploiters and compare life-history traits of mutualists and exploiters.

Keywords: mutualism, exploitation, competition, coexistence, adaptive dynamics, coevolution.

Introduction

Mutualisms are increasingly recognized as playing a key role in ecosystem function and the delivery of major ecological services (Agrawal et al. 2007; Holland and Bronstein 2008). However, many, if not most, mutualisms are beset by other, nonmutualistic species. These “exploiters” take advantage of the commodities provided by one or more of the mutualists without providing any commodity in return (Bronstein 2001; Yu 2001). Well-studied examples of exploiters include bees, ants, and hummingbirds that feed on floral nectar but do not pick up or deposit pollen; nonpollinating seed parasites of obligately insect-pollinated yuccas and figs; ants that consume food rewards produced by plants and other insects without defending their associates; and Rhizobium bacteria that fail to fix nitrogen for their legume hosts (e.g., Cook and Rasplus 2003; Tillberg 2004; Dede and Delaplaine 2005; Sachs and Simms 2008). In addition to being numerically abundant and taxonomically diverse, exploiters have been found to be evolutionarily persistent in both facultative and obligate mutualisms (Machado et al. 1996; Després and Jaeger 1999; Pellmyr and Leebens-Mack 1999; Currie et al. 2003).

This empirical evidence for the ubiquity of exploitation, however, clashes with conceptual expectation. The net effect of exploiters can be distinctly detrimental to one or both mutualists. Consequently, it has been argued that mutualist-exploiter associations should be rare in nature for both ecological reasons (e.g., exploiters would invade and drive mutualists to extinction) and evolutionary reasons (e.g., under the pressure of exploitation, natural selection would disfavor investments into mutualistic traits; Axelrod and Hamilton 1981; Bull and Rice 1991; Maynard Smith and Szathmáry 1995; Doebeli and Knowlton 1998; Herre et al. 1999; Denison 2000; Edwards and Yu 2007; Johnstone and Bshary 2008).

While progress has been made in explaining how mutualists are able to resist the “temptation to defect” (Frank 1994; Ferrière et al. 2002; West et al. 2002; Foster 2004; Holland et al. 2004; Foster and Kokko 2006; Foster and Wenseleers 2006; Kiess and van der Heijden 2006), there is a comparative paucity of theory explaining the evolutionary persistence of mutualisms in the presence of separate exploiter species. Nonetheless, several theoretical steps have been taken toward solving this ecological and evolutionary conundrum. The mathematical analyses of Law et al. (2001), Ferrière et al. (2002), Bronstein et al. (2003), Morris et al. (2003), and others have identified...
conditions based on trait values and on ecological details under which exploited mutualisms are ecologically viable. An emerging principle from these studies is that intra- and interspecific competition for commodities provided by the partner species is key for the coexistence of mutualists and exploiters.

The ecological interactions of mutualists and exploiters are expected to generate strong selective pressures on the mutualists (Ferrière et al. 2007) and to cause reciprocal selection on the exploiters. In turn, the coevolutionary process is likely to play a significant role in shaping the ecological dynamics of the system (Thompson 1998; Fussmann et al. 2007). Because competition, both intra- and interspecific, is a cornerstone of natural selection, it is likely to propagate feedbacks between the ecological and the evolutionary dynamics of mutualist-exploiter systems. Thus, our understanding of the ecology and evolution of exploited mutualisms requires an integrated theory of eco-evolutionary feedbacks mediated by intra- and interspecific competition.

Pollinating seed parasite mutualisms provide an ideal model system for an eco-evolutionary theory of exploited mutualisms. These are obligate interactions between flowering plants (the host), pollinating seed parasites (the mutualist), and nonpollinating seed parasites (the exploiter; Dufay and Anstett 2003). The best-known examples involve figs and yuccas, in which seed production by the plant is dependent on the pollination services of (with few exceptions) a single species of insect (fig wasp, yucca moth) that both pollinates and deposits offspring on its host plant. In addition, both figs and yuccas are exploited by one or more species of nonpollinators, each of which is associated with one or at most a few species of plant hosts. Exploiters depend on the pollinators either because inflorescences that have not been pollinated are aborted by the plant, along with developing exploiter larvae (in figs), or because pollinators fertilize the seeds on which exploiter offspring feed (in yuccas). Pollinating seed parasite mutualisms are among the best-studied examples of exploitation. Most of the currently available phylogenetic evidence for coevolution in mutualist-exploiter systems has been drawn from these systems (Machado et al. 1996; Pellmyr et al. 1996; Desprès and Jaeger 1999), and enough is known about their natural history to permit realistic features of their biology to be built into mathematical population models. The species-specific, obligate nature of the interaction for all three species means that, by contrast with more diffuse interactions, models that include only three species can account for significant features of the ecological and evolutionary dynamics.

In pollinating seed parasite mutualisms, pollinator and exploiter larvae develop at the expense of seeds within the same fruit or inflorescence; as a result, larvae of both species may experience exploitation competition and interference competition from both conspecific and heterospecific larvae (Jaeger et al. 2001; Marr et al. 2001; Peng et al. 2005). The role of such intra- and interspecific competition in promoting three-species ecological viability has been demonstrated by ecological models (Bronstein et al. 2003; Morris et al. 2003; Wilson et al. 2003). In these models, the critical parameters for species coexistence are the birth rates of mutualists and exploiters, parameters that also determine the number of larvae potentially competing for seeds within a fruit or inflorescence. We build on this body of ecological theory by treating the mutualist and exploiter birth rates as adaptive phenotypic traits subject to heritable variation and selection generated by ecological interactions. Given the intensity of intra- and interspecific competition, mutualist and exploiter birth rates determine the ecological state of the system and thus the selection pressures acting on heritable variation in the birth rates. As the birth rates respond to selection and evolve, the ecology of the system changes, closing the eco-evolutionary feedback loop. The analysis of this feedback loop enables us to answer three general questions: How does the evolutionary history of the mutualism influence its ability to sustain invasion by exploiters and form an ecologically viable interaction with them? How and by how much does the coevolutionary process change the phenotypes of the mutualist and the exploiter? What are the consequences of mutualists’ and exploiters’ coevolution for their ecological stability and population dynamics?

Methods

Morris et al. (2003) presented an ecological model of an obligate pollinating seed parasite mutualism exploited by a nonpollinating seed parasite species and found the conditions, with respect to pollinator and exploiter birth rates, under which coexistence of all three species is possible. We extended this ecological model by expanding the analysis of the role of competition in the population dynamics. We then embedded the ecological model in an evolutionary framework in order to analyze the patterns and consequences of coevolution between pollinator and exploiter birth rates.

Our analysis rests on three important assumptions. First, mutations affecting pollinator and exploiter birth rates are rare and have small effects; nevertheless, all trait values are accessible through mutation. This assumption allows us to link population dynamics and trait evolution by using the adaptive-dynamics framework (Metz et al. 1992; Dieckmann and Law 1996; Champagnat et al. 2006). Second, the evolution of birth rates is constrained by the fundamental trade-off between egg number and egg provisioning (e.g., Smith and Fretwell 1974); as a conse-
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et inter rate ar et of the of the plant allows coefficient on a at The trade-off (the pollinator the slope the (plant allows coevolve at birth) rate are assumed to suffer a cost during competition with their conspecifics because of, for example, their smaller size (e.g., Fox et al. 2001). Third, because of the difference in pollinator and exploiter phenology (Kerdelhué and Rasplus 1996; Pellmyr et al. 1996; Marr et al. 2001), pollinator larvae enjoy a competitive advantage over exploiter larvae that is independent of the species’ birth rates (Morris et al. 2003). Thus, the pattern of interspecific competition is fixed, and our analysis focuses on eco-evolutionary dynamics with respect to variation in pollinator and exploiter intraspecific competition.

On the basis of these assumptions, we construct a two-species (plant and pollinator) model to study the evolution of pollinator birth rate in the absence of an exploiter; by doing so, we identify the likely state of the mutualism before exploiter invasion. Next, we extend this model to include ecological interaction and coevolution with the exploiter. This three-species model allows us to predict (1) the phenotypes of exploiters that could invade and subsequently coevolve with the pollinator, (2) the consequences of the pollinator-exploiter coevolutionary dynamics for long-term coexistence, and (3) the phenotypic and population outcomes of the coevolutionary process, and it allows us to investigate how these predictions are affected by the intensities of pollinator and exploiter intraspecific competition.

Eco-Evolutionary Model in the Absence of an Exploiter

In the absence of an exploiter, the plant/pollinator interaction involves pollination and oviposition by one pollinator species visiting the flowers of one plant species. Larvae develop at the expense of seeds. The ecological dynamics of plant and pollinator are given by the per capita growth equations

$$\frac{1}{P} \frac{dP}{dt} = b_p M (1 - M)(1 - P) - 1,$$  \hspace{1cm} (1a)

$$\frac{1}{M} \frac{dM}{dt} = b_{M} P (1 - \mu M) - d_{M},$$  \hspace{1cm} (1b)

Here, $P$ and $M$ are the population densities of the plant and the pollinator (mutualist), respectively; $b_p$, $b_{M}$, $d_p$, and $d_{M}$ are the respective intrinsic birth and death rates; and $\mu$ is the intensity of mutualist intraspecific competition. The densities and birth rates incorporate subparameters such as numbers of sites for plants, potential oviposition sites, sites searched by pollinators, and the proportion of pollination events that are combined with oviposition. Furthermore, time and the pollinator death rate have been rescaled according to the plant death rate (see Morris et al. 2003). In the dimensionless version given above, the per capita population growth of plants is determined by the intrinsic birth rate ($b_p$), the availability of pollinators (the $M$ term), seed destruction by pollinator larvae (the $(1 - M)$ term), competition between plants for space (the $(1 - P)$ term), and death (at a normalized rate of 1). Since competition among plants is directly related to the proportion of free space in the environment, no coefficient is used to modify the intensity of competition. The per capita population growth of pollinators is determined by the intrinsic birth rate ($b_{M}$), the availability of plants (the $P$ term), competition between larvae for seeds (the $(1 - \mu M)$ term), and death (at the rate $d_{M}$).

Equations (1) were solved to find the equilibrium densities of the two species. All cases had a nontrivial two-species equilibrium. At this equilibrium, the invasion fitness (i.e., population growth rate when rare; Metz et al. 1992) of a pollinator with a mutant intrinsic birth rate $b_{M}^{\text{mut}}$ competing with the resident population of pollinators with the rate $b_{M}$, is

$$W_{M}(b_{M}^{\text{mut}}, b_{M}) = b_{M}^{\text{mut}}\frac{\hat{\nu}}{\nu}(1 - [\mu + \nu(b_{M}^{\text{mut}} - b_{M})]\hat{M} - d_{M},$$  \hspace{1cm} (2)

where $\hat{\nu}$ and $\hat{M}$ are the densities of plants and pollinators, respectively, at the ecological equilibrium given by equations (1) and are also functions of the trait value $b_{M}$. Equation (2) incorporates the assumed trade-off between fecundity and competitive ability. The competitive effect of any resident-type individual on a focal individual is measured by $\mu$ if the focal individual is of the resident type and by $[\mu + \nu(b_{M}^{\text{mut}} - b_{M})]$ if the focal individual is a mutant. Thus, if the mutant’s birth rate is higher than the resident’s, the competitive effect experienced by the mutant is increased by an amount taken to be proportional (for simplicity) to the difference between birth rates; if the mutant birth rate is lower than the resident’s, the competitive effect experienced by the mutant is reduced by that amount. The proportionality coefficient, $\nu$, measures the slope of the fecundity-competition trade-off that constrains the evolution of the mutualist birth rate; it is assumed to be species specific and constant.

Values of $b_{M}$ where the selection gradient $(\partial W_{M}/\partial b_{M}^{\text{mut}})(b_{M}, b_{M})$ is equal to 0 are called “evolutionary singular states” (Geritz et al. 1997). An evolutionary singular state at which $W_{M}$ is a maximum is an evolutionarily stable state (ESS). At the ESS, the resident population cannot be invaded by any (nearby) mutant. Evolutionary stability (as opposed to evolutionary branching) and evolutionary convergence were systematically tested by constructing and inspecting pairwise invasibility plots (Geritz et al. 1997).
Eco-Evolutionary Model in the Presence of an Exploiter

Once the system has been invaded by an exploiter species, both pollinator and exploiter larvae destroy seeds, but the exploiter does not contribute any additional pollination. The ecological dynamics of the three-species community are given by

\[
\begin{align*}
\frac{1}{P} \frac{dP}{dt} &= b_p M (1 - M)(1 - E)(1 - P) - 1, \\
\frac{1}{M} \frac{dM}{dt} &= b_m P (1 - \mu M) - d_M, \\
\frac{1}{E} \frac{dE}{dt} &= b_E PM (1 - M)(1 - \alpha E) - d_E,
\end{align*}
\]

where the symbols for plants and mutualists are the same as in equations (1), \( E \) denotes the exploiter population density, and \( \alpha \) is the intensity of exploiter intraspecific competition. The per capita population growth of exploiters is determined by the intrinsic birth rate \( (b_E) \), the availability of pollinated plants (the \( PM \) term), intraspecific competition with pollinator larvae for seeds (the \( (1 - M) \) term), intraspecific competition between exploiter larvae for seeds (the \( (1 - \alpha E) \) term), and death (at the rate \( d_E \)). Plants suffer seed loss from exploiter larvae (the \( (1 - E) \) term) in addition to pollinator seed destruction. Importantly, the exploiter species requires both plant and pollinator for its own survival. The model incorporates our assumption about intraspecific competitive superiority of mutualists over exploiters: the pollinator growth rate is not directly affected by the presence of an exploiter (eq. [3b]), whereas the exploiter growth rate is limited by interspecific competition with mutualists (eq. [3c]). The interspecific competition coefficient is normalized to 1 (hence the term \( (1 - M) \) in eq. [3c]), which sets the scale for the coefficients of intraspecific competition in mutualists (\( \mu \)) and exploiters (\( \alpha \)).

The ecological model specified by equations (3) has three potential types of solution: coexistence of all three species, exclusion of the exploiter, and extinction of all three species. Each outcome corresponds to a region in the space of the evolving traits \( b_m \) and \( b_E \). In all combinations of positive intraspecific competition intensities \( \mu \) and \( \alpha \) explored, coexistence was possible over some region of pollinator and exploiter birth rates, and the coevolution of pollinator and exploiter species could be investigated. Again, the intrinsic birth rates were allowed to evolve according to the invasion fitnesses

\[
W_s(b^{mut}_M, b_M) = b_M^m \hat{P}(1 - [\mu + \mu'(b^{mut}_M - b_M)\hat{M}]) - d_M, \quad (4a)
\]

\[
W_e(b^{mut}_E, b_E) = b_E^m \hat{P}M(1 - \hat{M})(1 - [\alpha + \alpha'(b^{mut}_E - b_E)\hat{E}]) - d_E. \quad (4b)
\]

Equation (4a) is identical to equation (2), except that here the densities \( \hat{P} \) and \( \hat{M} \) are evaluated at the three-species ecological equilibrium given by equations (3) and thus depend on both \( b_M \) and \( b_E \). Invasion fitness for a mutant exploiter with trait value \( b^{mut}_E \) is affected by the same fecundity-competition trade-off, this time with the trade-off slope \( \alpha' \). The quantity \( \hat{E} \) is the density of the exploiter at the ecological equilibrium given by equations (3). In the two-dimensional trait space \((b_M, b_E)\), the curves where the selection gradients \((\partial W_s/\partial b^{mut}_M)(b_M, b_M)\) and \((\partial W_e/\partial b^{mut}_E)(b_E, b_E)\) become 0 define the selective isoclines of the coevolutionary system. Points of intersection of the isoclines define the system’s coevolutionary singularities; they are potential coevolutionarily stable states (coESS), that is, combinations of \( b_M \) and \( b_E \) that are evolutionarily stable for both the mutualist and the exploiter. The attractivity and stability of the coevolutionary singularities can be studied by constructing the canonical equations of the trait dynamics based on the selection gradients (Dieckmann and Law 1996; see the appendix in the online edition of the American Naturalist).

Results

As described by Morris et al. (2003), the population dynamics of the three-species community given by equations (3) depend on the birth rates of the pollinator and the exploiter, \( b_M \) and \( b_E \), respectively. Three-species extinction occurs at low \( b_M \) values, three-species coexistence at intermediate \( b_M \) and \( b_E \) values, and exclusion of the exploiter at low \( b_E \) values (fig. 1). Morris et al. (2003) demonstrated that the equilibria are stable except in a narrow band of the three-species coexistence region bordering the extinction region, in which there is oscillation around an unstable equilibrium.

Varying the intensities of pollinator and exploiter intraspecific competition, \( \mu \) and \( \alpha \), changes the range of pollinator and exploiter birth rates that lead to each type of ecological outcome (fig. 1). In agreement with Morris et al.’s (2003) conclusions, we find that the three-species coexistence region widens into the exclusion region with increases in pollinator intraspecific competition, \( \mu \) (e.g., cf. fig. 1A, 1B, and 1C), and into the extinction region with increases in exploiter intraspecific competition, \( \alpha \) (e.g., cf. fig. 1I, 1F, and 1C). Thus, the major ecological
effect of increasing pollinator competition is to make the mutualism more amenable to ecological coexistence with exploiters that would otherwise be excluded; the major ecological effect of increasing exploiter competition is to “tame” exploiters that would otherwise cause three-way extinction. Altogether, the likelihood that an invading exploiter can coexist with a given pollinator increases with increasing competition in both species.

What we learn from this purely ecological analysis is that both the adaptive traits $b_e$ and $b_m$ and the intraspecific competition intensities $\mu$ and $\alpha$ influence the ecological outcome of the mutualism-exploiter interaction. Therefore, evolution of the pollinator birth rate in the absence of exploiters sets the stage for an ecological invasion by exploiters, the outcome of which will depend on the exploiter birth rate and both intraspecific competition coefficients. While exploiter speciation is not explicitly modeled, the exploiter species may either arise from within the mutualism by a shift in oviposition time (described below) or arise elsewhere and then invade. In the case where invasion and three-way coexistence are possible initially, subsequent coevolution of the pollinator and the exploiter will change their birth rates as well as the ecological state of the interaction, possibly moving the system into the exclusion or even extinction region of adaptive traits $b_m$ and $b_e$.

**Pollinator Evolution and Exploiter Invasion**

How does pollinator evolution affect the success of exploiter invasion? To answer this question, we consider the evolution of pollinator birth rate in the absence of exploiters and examine the outcome of exploiter invasion in a population at the pollinator’s evolutionary equilibrium.
We call the stable evolutionary equilibrium reached by the pollinator’s birth rate in the absence of exploiters the “mutualism-only” evolutionarily stable state (ESS).

Equation (2) yields the mutualism-only ESS as a function of pollinator competition. Evolution to an ESS, and generally to a low birth rate, is a consequence of the fecundity-competition trade-off. Except when the intensity of pollinator competition is low, pollinator evolution drives the system near the tapered end of the region of ecological coexistence with potential exploiters (fig. 1). More precisely, the mutualism-only ESS is always at the point where the pollinator coevolutionary isocline intersects the exploiters exclusion boundary (below this boundary, replace population density goes to 0, making the three-species system and the two-species system formally equivalent). At the mutualism-only ESS, exploiters with a birth rate lower than the pollinator’s are always excluded. Which exploiters can invade at the mutualism-only ESS depends on the intensity of intraspecific competition in both pollinators and exploiters. At lower intensities of pollinator intraspecific competition, exploiters must have a higher birth rate in order to successfully invade, while at higher intensities of exploiters intraspecific competition, exploiters with a wider range of birth rates can invade (fig. 2).

The case of an exploiter that has the same birth rate as the pollinator is interesting because it highlights the scenario in which an exploiter species arises via a change in the timing of oviposition with no difference in birth rate. Delaying oviposition changes the competitive environment experienced by larvae, which is the only feature that distinguishes pollinator and exploiter growth rates in our model. Later oviposition also eliminates the opportunity for pollination; the lack of selection on active pollination could then lead to secondary loss of pollination behavior in nascent exploiters. The model shows that invasion by such a “derived exploiter” is essentially determined by the intensity of pollinator competition and is possible only above a certain threshold (estimated to be $\mu = 1.1$; fig. 3; see also fig. 1C, 1F, 1H).

\textbf{Mutualism-Exploiter Evolutionary Persistence}

Given the successful invasion and ecological persistence of an exploiter, we now examine the subsequent coevolution of pollinator and exploiter birth rates and its consequences for the long-term viability of the three-species interaction. Evaluating equations (4) for different intensity of pollinator and exploiter intraspecific competition ($\mu$ and $\alpha$ between 0 and 2), we find that selection on birth rate can lead to a coevolutionarily stable state (coESS) within the three-species coexistence region. In this case, there is evolutionary persistence of the three-species community (fig. 1A–1F, 1H). However, there are two alternatives to evolutionary persistence. In one, coevolution leads to the boundary of the exploiter exclusion region (fig. 1G): the exploiter becomes extinct while the mutualism remains intact. We refer to the extinction of the exploiter after coevolution as “evolutionary purging” of the exploiter because the exploiter is driven to competitive exclusion by the coevolving pollinator. Once evolutionary purging occurs, the mutualism will begin to return to the mutualism-only ESS. In the second alternative to evolutionary persistence, coevolution leads to the boundary of the three-species extinction region and consequently to the extinction of all three species (fig. 2I). This is a case of “evolutionary suicide,” or evolution to extinction, in which the selection gradient drives a species to acquire nonviable trait values (Ferrière 2000; Gyllenberg and Parvinen 2001; Dieckmann and Ferrière 2004).

Evolutionary coexistence occurs over a wide range of pollinator and exploiter competition intensities (figs. 1, 3). Nevertheless, figure 3 demonstrates that evolutionary purging of the exploiter is the expected outcome for weak
intraspecific competition in both pollinator and exploiter, and evolutionary suicide is expected for strong pollinator competition and weak exploiter competition. These findings show that intensities of intraspecific competition that allow ecological coexistence between mutualists and exploiters do not guarantee evolutionary persistence (fig. 1G, 1I). On the other hand, intensities of intraspecific competition that restrict ecological coexistence to a small range of phenotypes may yet promote the evolutionary persistence of the three-species community (fig. 1A, 1D).

Phenotypic and Population Outcomes of Pollinator-Exploiter Coevolution

The intensity of intraspecific competition in pollinators is the main determinant of the phenotypic and population outcomes of coevolution with the exploiter (fig. 4). The coevolutionary process always drives the birth rate of the pollinator to a coESS value larger than the mutualism-only ESS value (fig. 4B). Pollinator and exploiter coESS birth rates vary predictably, yet nonmonotonically, with pollinator intraspecific competition (fig. 4A): they decrease as pollinator competition intensity \( \mu \) increases to \( \sim 1 \) and then increase gradually. The difference between pollinator and exploiter coESS birth rates is about twofold when pollinator competition is strong (\( \mu > 1 \)) and is greatest, up to tenfold, when pollinator competition is weak (\( \mu < 1 \); fig. 4A). In some cases, the coevolved exploiter birth rate is so high that the coevolved exploiters would have caused three-species extinction had they invaded the ancestral mutualism. Thus, coevolution has the potential to generate “kamikaze exploiters,” that is, those that can cause local extinctions of the mutualism upon invading naive, non-coevolved populations (fig. 3).

The equilibrium densities of the coevolved pollinator, exploiter, and plant populations also show strong nonlinear patterns of covariation with the intensity of pollinator competition, \( \mu \) (fig. 4C, 4E). Below \( \mu = 1 \), relaxing pollinator competition results in a strong increase of pollinator coESS population density (fig. 4C), while both exploiter and plant coESS population densities experience a marked decline (fig. 4C, 4E). Above \( \mu = 1 \), intensifying pollinator competition results in a decrease of the pollinator coESS population density (fig. 4C), while both exploiter and plant coESS population densities decrease more slowly (fig. 4C, 4E). Coevolution between pollinators and exploiters reduces plant population density from the ESS to the coESS (fig. 4F) but leads to remarkably little change in the pollinator population density from the ESS to the coESS (fig. 4D) in spite of having a significant effect on pollinator birth rate (fig. 4B).

The phenotypic and population outcomes of coevolution with respect to pollinator competition intensity are summarized in figure 5A. The observed patterns (fig. 5A) result from a combination of ecological and evolutionary effects (fig. 5B), the relative importance of which can be evaluated from our model. Ecological effects of varying pollinator competition intensity, \( \mu \), can be predicted from the ecological model, equations (3). Although no analytical results are available, a numerical approach is straightforward, and the results are displayed in figure 2A in the online edition of the American Naturalist. Evolutionary effects can be predicted from the selective gradients, equations (4), which yield expressions of the coESS birth rates \( b_m^* \) and \( b_e^* \) with respect to intraspecific competition intensities, \( \mu \) and \( \alpha \), and pollinator and exploiter equilibrium densities, \( M \) and \( E \):

\[
b_m^* = \frac{1}{\mu} \left( \frac{1}{M} - \mu \right), \tag{5a}
\]

\[
b_e^* = \frac{1}{\alpha} \left( \frac{1}{E} - \alpha \right). \tag{5b}
\]

By varying \( \mu \) and holding the birth rates \( b_m^* \) and \( b_e^* \) constant in equations (3), we find that \( \mu \) has primary (i.e., direct) ecological effects on the equilibrium population densities \( M \) and \( E \) (fig. 2A); meanwhile, by varying \( \mu \) and
Figure 4: Phenotypic and population outcomes of mutualist-exploiter coevolution with respect to the intensity of mutualist intraspecific competition ($\mu$). Exploiter competition is held constant at $\alpha = 0.6$ (gray lines) and $\alpha = 1.4$ (black lines). A, Mutualist (solid lines) and exploiter (dashed lines) birth rates at the coevolutionarily stable state (coESS). B, Difference between mutualist birth rates at the coESS and at the mutualism-only evolutionarily stable state (ESS). C, Mutualist (solid lines) and exploiter (dashed lines) population densities at the coESS. D, Difference between mutualist population densities at the coESS and at the ESS. E, Host population density at the coESS. F, Difference between host population densities at the coESS and at the ESS. Parameter values are as in figure 1.
Figure 5: Ecological and evolutionary effects of decreasing mutualist intraspecific competition ($\mu$) on adaptive traits (mutualist birth rate $b_M$ and exploiter birth rate $b_E$) and population densities (mutualist density $M$, exploiter density $E$, and host density $P$) at the coevolutionarily stable state. A, Observed ecological and evolutionary effects, summarized from figure 4. B, Predicted primary and secondary ecological and evolutionary effects. Primary ecological effects are responses of equilibrium population densities to varying $\mu$ while holding traits constant; they can be predicted from equations (3) (see also fig. A2 in the online edition of the American Naturalist). Primary evolutionary effects show the selective effect on the adaptive traits of varying $\mu$ while holding population densities constant; they can be predicted from equations (5). Secondary ecological effects are changes in equilibrium population densities resulting from changes in trait values, independent of the direct changes caused by varying $\mu$; they can be predicted from equations (3) (and fig. A2). Secondary evolutionary effects are changes in adaptive traits caused by changes in population densities, estimated independently of the direct selective effect of varying $\mu$; they can be predicted from equations (5).

Forcing the ecological equilibrium population densities $\hat{M}$ and $\hat{E}$ to be constant in equations (5), we find that $\mu$ has primary evolutionary effects on the coESS birth rates $b^*_M$ and $b^*_E$. In addition, the primary ecological effects of $\mu$ cause secondary (i.e., indirect) evolutionary effects on the coESS birth rates $b^*_M$ and $b^*_E$ that can be predicted from equations (5) by varying the equilibrium population densities $\hat{M}$ and $\hat{E}$ while keeping $\mu$ constant. Furthermore, the primary evolutionary effects of $\mu$ cause secondary ecological effects on the equilibrium population densities $\hat{M}$ and $\hat{E}$ that can be predicted from equations (3) by varying the pollinator and exploiter birth rates $\hat{b}_M$ and $\hat{b}_E$ while holding $\mu$ constant (fig. A2).

How much variation in equilibrium traits and population densities is explained by ecology versus evolution as pollinator competition intensity varies? This question can be answered by comparing the observed outcomes of the coevolutionary process (fig. 5A) with the predicted primary and secondary ecological and evolutionary effects (fig. 5B). Primary and secondary ecological effects appear to be entirely congruent in direction at both low and high $\mu$. However, they do not explain the strong decrease in plant population density $\hat{P}$ when $\mu$ decreases at low $\mu$ or the quasi absence of change in exploiter population density $\hat{E}$ at high $\mu$. Thus, more complex effects of eco-evolutionary feedbacks must play a significant role. The observed response of the pollinator birth rate at low $\mu$ is consistent with a strong primary evolutionary effect, which opposes and overcomes the secondary evolutionary response. In contrast, at high $\mu$, it is the secondary evolutionary effect of changing $\mu$ that explains the observed change in pollinator birth rate; the primary evolutionary
effect has only a moderating effect. Likewise, only the secondary evolutionary effect can explain the observed dramatic change in exploiter birth rate at low $\mu$. At high $\mu$, the decrease in exploiter birth rate as $\mu$ decreases is explained neither by primary nor by secondary evolutionary effects. Again, more complex effects of eco-evolutionary feedbacks must be involved.

Discussion

The mutualism-exploitation interaction is an important model system because it provides a test case in which to move coevolutionary theory beyond a pairwise perspective. Coevolution is increasingly recognized as involving groups rather than pairs of species; furthermore, the presence of other species is being shown empirically to alter the outcome of pairwise, coevolving interactions (e.g., Currie et al. 2003; Strauss et al. 2005; Thompson and Fernandez 2006; Thrall et al. 2007). Thus, multispecies coevolution has the potential to be a powerful organizing force within ecological communities. A logical way to begin to incorporate multiple species within coevolutionary models is to explore the eco-evolutionary effects of third species that closely interact with well-understood, coevolving, pairwise interactions, a research direction that has been opened only recently by theorists (Gandon 2004; Nuismer and Doebeli 2004; Ferrière et al. 2007).

In order to investigate the eco-evolutionary dynamics of an exploited mutualism, we constructed an adaptive-dynamics model of the coevolution of mutualist and exploiter birth rates, given a fecundity-competition trade-off and using the ecological dynamics described by Morris et al. (2003). Our model assumes complete competitive dominance of the mutualist species over the exploiter due to a gap between oviposition times. Therefore, we fixed the intensity of interspecific competition from mutualists experienced by exploiters and focused on examining the role of mutualist and exploiter intraspecific competition in the state of the mutualism at the time of exploiter invasion, in the coevolutionary process, and in the phenotypic and population consequences of eco-evolutionary feedbacks. We found that intraspecific competition does make long-term coexistence possible. Once an exploiter has successfully invaded the mutualism, high intensities of mutualist and exploiter intraspecific competition make it more likely that a stable coevolutionary equilibrium will be reached at which the host, mutualist, and exploiter coexist. When the intensity of exploiter intraspecific competition is low, evolutionary suicide will occur, with all three species becoming extinct. When the intensity of mutualist intraspecific competition is low, the exploiter is excluded from the community through evolutionary purging, a type of coevolutionary dynamic not previously identified in mutualism-exploiter interactions (but see Kooi and Troost 2006 for evolutionary purging of a competitor).

When long-term coexistence occurs, ecological and evolutionary processes interact to determine phenotypic and population outcomes, with feedbacks between ecological and evolutionary responses playing a significant role. Under weak mutualist competition, the exploiter’s high birth rate is produced by secondary evolutionary effects, while the host’s low density results from more complex effects of eco-evolutionary feedbacks. Under strong mutualist competition, coevolution leads to a minimal difference in birth rate between mutualist and exploiter, and the host density is highest. We have shown that neither primary nor secondary ecological or evolutionary effects suffice to explain this pattern.

Below, we discuss the implications of our results for understanding the dynamics of mutualist-exploiter communities. We emphasize insights that can be applied to coevolution in general.

Origin of Exploiters: Assembled or Derived?

The model predicts that in the absence of exploiters, the mutualist species evolves to a relatively low birth rate as a consequence of a fecundity-competition trade-off. Evolution of the mutualist is likely to produce an interaction that is ecologically more stable than the ancestral mutualism because the low cost imposed on hosts by evolved mutualists results in a larger host population. On the other hand, evolving to a low birth rate also means evolving to a trait region in which three-species extinction is more likely after an exploiter invasion. However, early invasion of the mutualism by exploiters can “immunize” the mutualism against more harmful exploiters that would cause three-species extinction, a process that is emerging as an important mechanism maintaining cooperation and mutualism (Nowak and Sigmund 1998; Foster and Kokko 2006; Ferrière et al. 2007). These results suggest that exploiters should often be anciently associated with mutualisms, such as in the attine ant–fungus mutualism (Currie et al. 2003) and the fig–fig wasp mutualism (Machado et al. 1996), in which exploiters are known to have persisted for millions of years. Unrelated exploiters that have invaded a mutualism recently may have already been “tamed” because they have coevolved with a closely related mutualist pair (Lopez-Vaamonde et al. 2001; Currie et al. 2003; Segraves and Pellmyr 2004).

Our model also suggests that exploiters may be derived from the mutualist species, for example, by a shift in oviposition time, as has been proposed in the yucca (Pellmyr et al. 1996; Pellmyr and Leebens-Mack 2000) and globe-flower (Després and Cherif 2004) mutualisms (see also Law et al. 2001). Invasion by a derived exploiter is not
predicted to cause the immediate extinction of the mutualism at any point during evolution of the mutualist. The model predicts that strong mutualist intraspecific competition is the key condition for derived exploiters to be able to persist in the mutualism. When mutualist competition is weak, derived exploiters can never arise, and exploiters are predicted to be assembled. When mutualist intraspecific competition is strong, derived exploiters can arise at any time in the mutualist’s evolutionary history. This prediction agrees with the suggestion that escape from strong intraspecific competition was the mechanism behind the radiation of nonpollinators from pollinators in the globeflower–globeflower fly mutualism (Desprès and Jaeger 1999; Desprès and Cherif 2004).

Dynamics of Mutualist-Exploiter Coevolution

In our three-species model, the long-term persistence of the mutualism is achieved through evolutionary purging of the exploiter or else through mutualist-exploiter coevolution toward an ecologically viable three-species equilibrium. Surprisingly, wide ranges of trait values that permit ecological coexistence between mutualists and exploiters do not guarantee evolutionary persistence; meanwhile, a narrow range of trait values allowing for ecological coexistence is no indication that evolutionary persistence is impossible.

Our results suggest that systems in which both mutualist and exploiter intraspecific competition are weak should be rare and, at best, evolutionarily transient because of evolutionary purging of the exploiter. Systems in which exploiter competition is weak and mutualist competition is strong should also be rare, in this case because of evolutionary suicide. Thus, the intensity of intraspecific competition can be critical for long-term mutualist-exploiter coexistence. However, while there is empirical evidence that intraspecific competition in mutualists and exploiters does exist (Anstett et al. 1996; Bronstein et al. 1998; Jaeger et al. 2001; Jousselin et al. 2001) and theory suggesting that there should be selection on hosts to increase competition in mutualists and exploiters (Ferdy et al. 2002), there is as yet little information available about the relative intensities of intraspecific competition in mutualists and exploiters.

The model makes the key assumption of a spatially homogeneous community. However, spatial variation in environment, community composition, and evolutionary history can influence coevolutionary dynamics (Thompson 1999, 2005). Inspection of the model results suggests that the three-species system may be maintained as a meta-community even when coevolution should lead to extinction of the exploiter (evolutionary purging) or of all three species (evolutionary suicide). When evolutionary purging occurs, the exploiter becomes extinct locally and might be expected to do so globally as well. However, if populations linked by migration are at different evolutionary stages, exploiters may be able to persist by invading populations that are still susceptible. In this case, a species that should be eliminated by evolutionary dynamics (purging) could be maintained by an ecological mechanism (dispersal). Similarly, an entire system that should be eliminated by evolutionary suicide might be rescued by frequent recolonization of patches by hosts and mutualists, allowing temporary escape from exploiters. In either case, changes in migration rate or patch fragmentation could cause large changes in the eco-evolutionary outcome of the three-species interaction, as suggested by Urban et al. (2008).

Migration within metacommunities could also lead to local extinctions of the mutualism even when there is a viable three-species coESS. When exploiter intraspecific competition is low but exploiters are not purged, exploiters are expected to coevolve into “kamikazes” that will cause extinction of communities composed of mutualists that evolved in the absence of exploiters. Whether the entire system is driven to local extinction may depend on whether mutualists are obligate or facultative. For example, in the seed dispersal mutualism between conifers and crossbills, introduction of red squirrels (seed predators) from neighboring communities has driven crossbills (seed dispersers), but not black spruce, to local extinction (Parchman and Benkman 2002).

Another model assumption is a constant environment. Examination of figure 1 yields insight into how gradual environmental change or evolution of the host species can affect the eco-evolutionary dynamics of the system. If the intensity of mutualist intraspecific competition is altered by a changing environment (e.g., Memmott et al. 2007) or by evolution of host morphology (e.g., Ferdy et al. 2002), the system can move between evolutionary purging of the exploiter and evolutionary persistence. Intensifying mutualist intraspecific competition could also open the opportunity for invasion by derived exploiters. Meanwhile, changes in the intensity of exploiter intraspecific competition can shift the system between evolutionary suicide and evolutionary persistence.

Phenotypic Consequences of Mutualist-Exploiter Coevolution

We predict that mutualists coevolving with exploiters should always have a higher birth rate than mutualists that have evolved without exploiters. Similarly, Ferrière et al. (2007) predicted that mutualists evolve lower rates of investment into the mutualism when in the presence of exploiters. While there are mutualisms with only partial geographic overlap with exploiters (Pellmyr and Leebens-
Mack 2000; Anderson 2006), comparisons between populations are still needed to determine the effect the presence of exploiters has had on mutualist evolution (e.g., Benkman 1999).

Exploiters with a birth rate lower than the mutualist’s can exist transiently; however, our model shows that coevolution always results in coevolved exploiters with a birth rate higher than that of the coevolved mutualist. The difference in coevolved birth rates is predicted to be minimal and fairly constant in systems where mutualist competition is strong but to diverge dramatically as mutualist competition decreases. In the globeflower and yucca mutualisms, more exploiter eggs than pollinator eggs are found per fruit (Pellmyr 1989; Addicott 1996). However, as both mutualists and exploiters can spread their eggs among multiple fruits, the differences in eggs per fruit may reflect differences in pollinator and exploiter population densities and in the numbers of inflorescences/fruits available at the time of oviposition rather than differences in fecundity.

In our model, intermediate birth rates evolve as a consequence of the fecundity-competition trade-off experienced by mutualists and exploiters. While we have used an intraspecific trade-off to understand the evolution of individual species, fecundity-competition trade-offs, and competition-colonization trade-offs more generally, have previously been applied to mutualistic communities only in order to explain interspecific coexistence (Yu et al. 2001; Stanton et al. 2002). Consequently, the shape and slope of this trade-off within mutualist and exploiter species require empirical investigation. In the absence of more empirical data, we assumed the same trade-off for both the mutualist and the exploiter (i.e., equal slopes, \( \mu = \alpha' \)), and we varied this slope (between 0 and 0.5) to test the robustness of our results. The qualitative ecological and evolutionary patterns reported here were unaffected except when the slope is 0 (results not shown). However, different eco-evolutionary dynamics might develop if the trade-off were to depart significantly from the assumed linearity (cf. eqq. [2] and [4]). With a sufficiently large degree of concavity, evolutionary branching might occur, as indicated by general theory (de Mazancourt and Dieckmann 2004; Rueffler et al. 2004) and a previous model of mutualism evolution (Ferrière et al. 2002). This is an interesting possibility that warrants future theoretical investigation, as it would predict persistent trait variation within mutualist and exploiter species and reveal new ways in which eco-evolutionary feedbacks mediated by phenotypically different populations within species could affect eco-evolutionary interactions between species.

**Population Consequences of Mutualist-Exploiter Coevolution**

The model shows that the response of coevolutionary equilibrium population densities of hosts, mutualists, and exploiters to variation in the intensity of competition is mediated by ecological and evolutionary forces and their interactions. Such a partitioning of ecological and evolutionary effects due to environmental change is germane to the trait-population time series analysis proposed by Hairston et al. (2005).

A significant response of relaxing mutualist intraspecific competition is a sharp decline in host density. This response is best explained by a synergistic interaction between primary ecological and primary evolutionary effects (i.e., the increases in mutualist density and mutualist birth rate as mutualist competition becomes weaker). The decrease in host population density at coevolutionary equilibrium in response to relaxed mutualist competition is part of a twofold “trait-abundance syndrome” that could not have been predicted unless eco-evolutionary feedbacks were accounted for. Under weak mutualist competition, the model predicts coevolution of associations of hosts with low density, mutualists with high density, and high-birth-rate exploiters with low density. Under strong mutualist competition, coevolution is expected to result in associations of hosts with high density and mutualists and exploiters with similar densities and a relatively small difference in birth rates. These trait-abundance syndromes have three counterintuitive implications. (1) Persistent, highly parasitic exploiters can be favored by coevolution. (2) Exploiters can evolve strong parasitism (i.e., a high birth rate), and yet the density of coevolved mutualists can be high. (3) Low plant density is caused primarily by the mutualist’s coevolved birth rate and high density, not by highly parasitic coevolved exploiters. Indeed, under weak mutualist competition, the coevolutionary process leaves host population density almost unchanged from its mutualism-only equilibrium population density.

**Concluding Remarks**

Our eco-evolutionary model of a mutualism-exploiter system highlights that exploiters are not just opportunistic visitors of little ecological or evolutionary relevance. The success or failure of their invasion reflects specific features of mutualist evolution. Persistent exploiters have significant evolutionary effects on mutualists and themselves change as mutualists evolve. The phenotype of mutualists and the abundance of hosts cannot be understood unless coevolution with exploiters is taken into account, and the ecological characteristics of each species (mutualist and exploiter) have eco-evolutionary repercussions on the
other species. By accounting for interactions between ecological and evolutionary processes, our model has delivered new predictions about the evolutionary history of mutualisms and the characteristics of coevolved mutualist-exploiter communities and new insights into the coevolutionary process in a community context. In order to evaluate these predictions, we are in need of empirical studies that identify and compare populations with and without exploiters and that directly compare life-history traits of mutualists and exploiters.

Extensions of the current theory are needed to determine whether exploited mutualisms can be maintained spatially when coevolution should otherwise lead to the extinction of one or more species and whether coevolution can still lead to stable three-species coexistence when the intensity of intraspecific competition changes as a result of environmental change or host evolution. An even broader theoretical perspective is opened by connecting our model to host-parasite coevolutionary theory. The model studied here has the structure of a one-host–two-parasite system, assuming a superinfection process between parasite populations and a single-infection process among genetic variants within parasite populations (Levin and Pimentel 1981; Nowak and May 1994; May and Nowak 1995; van Baalen and Sabelis 1995; Mosquera and Adler 1998). Our conclusions about long-term coexistence are consistent with host-parasite evolutionary theory, although the latter would predict coevolution of less-parasitic rather than more-parasitic mutualists and exploiters (Mosquera and Adler 1998; Pugliese 2002; Boldin and Diekmann 2008). We hypothesize that this fundamental difference is rooted in the mutualistic relationship that one of the parasites has with the host.

Current evolutionary theory views parasitism and mutualism as two ends of a phenotypic continuum (Yamamura 1993; Genkai–Kato and Yamamura 1999). Our analysis suggests that mutualism and parasitism should be investigated as separate characters that can evolve in a multidimensional trait space. This will pave the way for a deeper understanding of the ecology and evolution of complex, partly beneficial, partly antagonistic “liaisons dangereuses” (van Baalen and Jansen 2001; Selosse et al. 2006) in natural communities.

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