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Ecological Dynamics of Mutualist/Antagonist Communities

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abstract: One approach to understanding how mutualisms function in community settings is to model well-studied pairwise interactions in the presence of the few species with which they interact most strongly. In nature, such species are often specialized antagonists of one or both mutualists. Hence, these models can also shed light on the problem of when and how mutualisms are able to persist in the face of exploitation. We used spatial stochastic simulations to model the ecological dynamics of obligate, species-specific mutualisms between plants and pollinating seed parasite insects (e.g., yuccas and yucca moths) in the presence of one of two obligate antagonist species: flower-feeding insects (florivores) or insects that parasitize seeds but fail to pollinate (exploiters). Our results suggest that mutualisms can persist surprisingly well in the presence of highly specialized antagonists but that they exhibit distinctly different temporal and spatial dynamics when antagonists are present. In our models, antagonists tend to induce oscillations in the mutualist populations. As the number of per capita visits by antagonists increase, the system's oscillatory dynamics become more extreme, finally leading to the extinction of one or more of the three species. When the antagonists exhibit high per capita visitation frequencies and long dispersal distances, significant spatial patchiness emerges within these tripartite interactions. We found surprisingly little difference between the ecological effects of florivores and exploiters, although in general florivores tended to drive themselves (and sometimes the mutualists) to extinction at parameter values at which the exploiters were able to persist. These theoretical results suggest several testable hypotheses regarding the ecological and evolutionary persistence of mutualisms. More broadly, they point to the critical importance of studying the dynamics of pairwise interactions in community contexts.

Keywords: cheating, community, coexistence, exploitation, mutualism, population dynamics.

Understanding how interspecific interactions drive changes in the abundance and genetic composition of species has been a major goal of ecology and evolutionary biology for well over a century. To make empirical studies more feasible and theoretical studies analytically tractable, much of this work has focused on interactions between pairs of species, in isolation from the broader ecological community. Yet, extracting pairwise interactions from their community context is unrealistic at best and misleading at worst (Bronstein and Barbosa 2002; Stanton 2003). Most interactions are likely to be relatively weak and diffuse, such that removing any one partner species will have minimal effects on the species with which they associate (e.g., Paine 1992; Morris 2003). However, when some interspecific interactions are strong, slight changes in community context can quantitatively or qualitatively alter the outcomes of associations between any single pair of species, generating "apparent" interactions between species that do not interact directly, enhancing or diminishing interaction strengths, or even reversing the sign of the pairwise interaction (Worthen and Moore 1991; Bacher and Friedli 2002; Bronstein and Barbosa 2002).

Both the population dynamics and evolution of the key players in mutualisms are known to be affected by species other than single partners. First, in most mutualisms, each species interacts with a suite of comutualists, whose interactions with each other can alter pairwise benefits (Stanton 2003). Second, some associations are only mutually beneficial in the presence of another, nonmutualistic species. For example, in most protection mutualisms, benefits accrue to the protected species only when natural enemies are present; when they are absent, tenders confer either neutral or negative effects (e.g., Cushman and Whitham 1989; Buckley and Ebersole 1994). Third, natural enemies and other nonmutualistic species can alter the success of one and thus potentially both mutualists (e.g., Müller and Godfray 1999; Bacher and Friedli 2002). Fourth, the presence or absence of species involved in different kinds of mutualisms with one of the partners can alter the success of the focal mutualism. For example, mutualistic symbioses between leafcutter ants and certain bacteria increase the success of the mutualism between these ants and the fungi they cultivate (Currie et al. 1999). Finally, some of

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these additional associates are "exploiters" (also known as cheaters or parasites), species able to obtain the rewards or services one partner provides to the other while providing nothing in return (Bronstein 2001*b*).

In the study of mutualisms, the lack of a broad community perspective has been perpetuated by a somewhat myopic focus on highly specialized, obligate interactions. Examples of these mutualisms include certain insect pollination systems (Johnson and Steiner 2000), protection mutualisms in which myrmecophytic plants can only survive when ants defend them against their natural enemies (Palmer et al. 2003), and obligate nutritional mutualisms between unicellular symbionts and their hosts (Moran and Wernegreen 2000). Extreme specialization is clearly rare among most nonsymbiotic mutualisms (e.g., Waser et al. 1996; Hoeksema and Bruna 2000). However, specialized mutualisms offer undeniable advantages for studying many ecological and evolutionary phenomena, particularly when compared with diffuse mutualisms characterized by weaker selection pressures and a wider array of partner species. At present, in fact, much of our general understanding of the ecology and evolution of mutualism—including population dynamics (Holland et al. 2002), trait evolution (Aigner 2001), coevolution (Thompson and Cunningham 2002), and cospeciation (Weiblen and Bush 2002)—emerges from this small subset of interactions. We show in this article that they can also serve as models for exploring how the community context influences the ecological dynamics of mutualism.

Among the most thoroughly studied specialized mutualisms are plant/pollinator interactions in which a single insect acts as both pollinator and seed predator of a single plant species. The best known of these so-called pollinating seed parasite mutualisms are the fig/fig wasp and yucca/yucca moth interactions, although several similar but independently evolved interactions have been discovered in recent years (Dufaÿ and Anstett 2003). The antagonists associated with these mutualisms are also relatively well-known. They include predators and parasites of the insects, herbivores and florivores of the plants, and exploiters of the mutualisms. Exploiters feed on seeds fertilized by the pollinators but never pollinate the plants. Many of these antagonists are themselves species specific (e.g., Udovic 1986; Pettersson 1992; Pellmyr 1999; Weiblen and Bush 2002). Pollinating seed parasite mutualisms, both alone and in the presence of a single exploiter species, are proving amenable to ecological and evolutionary modeling (Holland and DeAngelis 2001, 2002; Law et al. 2001; Ferdy et al. 2002; Ferrière et al. 2002; Gomulkiewicz et al. 2003; Morris et al. 2003; Wilson et al. 2003), suggesting that they can serve as useful model systems for exploring how mutualisms function in different community contexts.

We have been exploring conditions under which pollinating seed parasite mutualisms can persist ecologically in the presence of obligate nonpollinating seed parasites (Morris et al. 2003; Wilson et al. 2003). Mutualisms are widely believed to be sensitive to extinction in the presence of exploiters like these unless exploitation is kept under relatively strict control (Axelrod and Hamilton 1981; Bull and Rice 1991; Yu 2001; Johnstone and Bshary 2002; West et al. 2002; but see Law et al. 2001; Ferrière et al. 2002). Our models suggest, however, that pollinating seed parasite mutualisms are remarkably resilient ecologically to the effects of these species. Under a wide range of realistic parameter values, exploiters are able to invade and then persist successfully alongside the mutualists. Coexistence of mutualists and exploiters is particularly facilitated in spatially structured situations by the formation of stable spatial patterns (Wilson et al. 2003). We briefly summarize these previous results in the "Discussion."

In our previous work, we examined the dynamical effects of exploiters of pollinating seed parasite mutualisms that consume fertilized ovules, that is, species that function as nonpollinating seed parasites. But there is more than one way to exploit the goods or services exchanged by mutualists without reciprocating. For example, florivores (defined here as species that consume flowers but that have no effect on future flowering or plant mortality) are in essence also acting as a form of exploiter. The difference is that whereas nonpollinating seed parasites consume ovules only after they have been fertilized by pollinators, florivores remove ovules before they can be visited by pollinators. As an initial step toward exploring how the dynamics of pollinating seed parasite mutualisms might depend on the community context, in this article we compare the effects of these two types of antagonists, nonpollinating seed parasites and florivores. Aside from the symmetry of considering antagonists that act before versus after the mutualistic interaction itself has taken place, this comparison has the additional attractive feature that both nonpollinating seed parasites and many common florivores are obligately dependent on the plant.

We address three related questions. First, are there any general effects of antagonists on the dynamics of an obligate mutualism that transcend the particular details of how exploitation occurs? Second, how well do the obligate antagonists themselves persist? Finally, do florivores and nonpollinating seed parasites inflict qualitatively different effects on these mutualisms, reflective of their contrasting natural histories? Our broader goal is to consider what we may learn about obligate mutualisms by examining how they function within minimally more complex community contexts.

Methods

Pollinating Seed Parasite Mutualisms and Their Antagonists

We briefly review the natural history of the yucca/yucca moth mutualism, the pollinating seed parasite interaction that most closely matches the conditions we have established in our models. We focus on features that relate explicitly to the models presented in this article. (For greater detail on the biology of these interactions, see Pellmyr 2003.)

Before and during the pollination stage, some proportion of flowers may be consumed by florivores. The best-studied florivores are beetle larvae (Nitidulidae) that feed obligately on buds and newly opened flowers of certain yucca species, leading them either to abort before pollination or to be avoided by pollinators (Udovic 1986; Huth and Pellmyr 1997); in either case, these flowers do not produce seeds.

Most yucca species (currently estimated at 70%) can only be pollinated by females of a single insect species, a moth of the genus *Tegeticula* or *Parategeticula* (Prodoxidae); in most of the handful of exceptions, one moth species is associated with two to three yucca species (Pellmyr 2003). On arrival at a plant, pollinators may lay one or more eggs in the flowers and then deposit pollen on the stigmas. Pollinator offspring feed on and destroy a fraction of the developing seeds. Subsequently, sometimes at a delay of 1 or more weeks, female exploiters arrive at the same plant and oviposit without pollinating. Exploiters are close relatives of the pollinators; they lack the morphological adaptations necessary for transferring pollen between flowers. Like the florivores, pollinator and exploiter adults spread their eggs across several flowers per plant and across several plants. Exploiter and pollinator offspring feed alongside each other, although pollinator larvae generally have a temporal advantage. Larvae are incapable of moving among fruits. Hence, pollinators and exploiters in the same fruit potentially compete for the same pool of seeds.

When pollinator and exploiter larvae have finished feeding, they depart the fruit and pupate near the plant. They mate on emergence as adults. Female mutualists and exploiters then disperse to deposit their eggs, a process that requires them to seek out new plant individuals in the correct flowering stage. Adults can fly surprisingly long distances at this stage (see "Discussion"). Seeds are dispersed by either wind or biotic vectors soon after the insects leave the fruit.

The natural history we have presented is also applicable in general outline to other pollinating seed parasite mutualisms, with several important distinctions. In certain other systems, for instance, more than one insect species is commonly associated with each plant species (the *Trollius*/*Chiastocheta* fly mutualism; Després et al. 2002); pollinating seed parasites coexist with other, unrelated pollinators (the *Lithophragma*/*Greya* moth mutualism; Gomulkiewicz et al. 2003); exploiter species are absent (the senita cactus/senita moth mutualism; J. N. Holland, personal communication); or pollinators deposit all of their eggs on a single plant (fig/fig wasp mutualisms; Bronstein 1992).

Spatial, Stochastic Simulation Model

Here we describe the rules of a simulation incorporating plants, insect florivores, pollinating insect mutualists (hereafter referred to as pollinators), and nonpollinating seed parasite insects (hereafter referred to as exploiters). The advantages of using a simulation model include the ability not only to add many detailed interactions but also to explicitly incorporate demographic stochasticity and spatial structure. As a result, we can examine how behavioral-scale processes affect population-level dynamics as well as compare the effects of different kinds of associates on the mutualism. Furthermore, comparisons between the results for spatial and nonspatial simulations indicate the importance of spatially distributed interactions for the ecological persistence of the multispecies system.

Figure 1 illustrates how the fates of ovules are affected by interspecific interactions that take place within a reproductive season. In our simulations, as in the yucca system, plants typically survive for many reproductive seasons. In contrast, individuals of the three insect species survive for only a single season. Population densities of insects and plants change between seasons as a result of interactions among species, and our results are presented at this temporal scale. However, the important ecological interactions take place at a much shorter behavioral timescale. These behavioral processes include production of flowers and ovules by the plants, attacks on flowers by florivores, pollination and oviposition by mutualist insects, and oviposition by exploiters. Interactions take place in precisely this order, with the products of one interaction establishing the condition of ovules for the next interaction across the entire population. Although the model incorporates all of these interactions, here we present results in which either the florivore or exploiter (but not both) is present, since we wish to compare the dynamical consequences of these two types of antagonists on the ecological persistence of the mutualism. Each of these interactions is described in detail below, and the relevant parameters for each are defined. Default parameter values are listed in table 1.

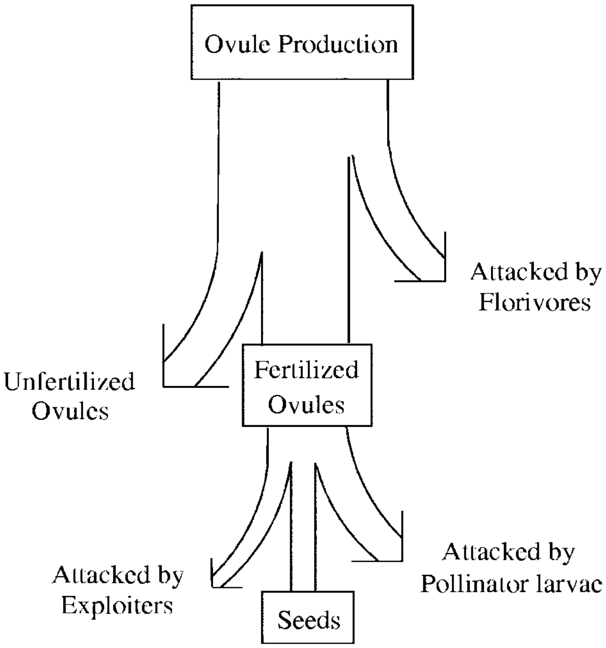

Figure 1: Characterization of the fate of ovules. All insect visits are assumed to follow Poisson distributions. Each florivore visits on average ε_F sites, each of which may harbor a single plant. All ovules that are encountered by florivores one or more times are destroyed. In a fraction γ of the visits each pollinator makes to flowers not consumed by florivores, its eggs survive to become larvae that consume the ovules. Fertilized ovules that escape attack by pollinator larvae develop into seeds if they are not attacked by larvae of exploiters. The average number of sites each pollinator and exploiter visits are β and ε_E, respectively.

Plants

Plants are distributed over a uniform environment represented by a two-dimensional square lattice with periodic boundaries (a torus). Although the connected opposite edges of periodic boundary conditions are clearly unrealistic from a biological standpoint, we use them here because they minimize edge effects when it is the dynamics of the interior region in a finite space that is of interest. On our lattice, we make the assumption that each site is occupied by at most one plant. Hence, germination sites are the ultimate factor regulating plant population growth. We refer to the density of plants, mutualists, exploiters, and florivores as *P*, *M*, *E*, and *F*, by which we mean the average number of individuals per site. Because a site can harbor at most a single plant, plant density is synonymous with the probability that a site is occupied by a plant.

Plant reproduction takes place as follows. We assume that with probability θ, a plant produces one flower containing one ovule during a reproductive season. To develop into a seed, an ovule must successfully survive through a long sequence of ecological interactions. First, the flower is subject to attack by a florivore, which destroys the ovule if it occurs. Second, provided that it survives the florivore onslaught, the ovule must be fertilized by a pollinator, but the offspring deposited by that pollinator must not survive to feed. Third, the developing seed must escape attack by ovipositing exploiters. If an ovule follows this pathway, then it will become a mature seed, which will then disperse to a randomly chosen site located within a distance Δ_P of its mother's location. After all seeds have been dispersed, each established plant may die with probability δ_P. Finally, seeds germinate on all empty sites and mature into plants capable of flowering the following season, with a maximum of one plant per site, and perish on sites that are occupied by existing plants.

Florivore Visits

Once ovules are produced by the plants, they become available for attack by female florivorous insects. During each season, each individual florivore visits a number of sites chosen from a Poisson distribution with mean ε_F. Between successive visits, an individual disperses to a new, randomly selected site located up to Δ_F lattice spacings away. If this site harbors a plant, the florivore attacks its flower. An attack consists of depositing an egg into the flower; the florivore larva subsequently consumes that flower in its entirety. Even if several florivore eggs are deposited into the same flower, only a single larva will mature. Florivore larvae are assumed to be competitively superior to pollinators, since florivores arrive first in the temporal sequence (fig. 1). After completion of all visits, adult florivores die.

Table 1: Parameters used in the plant/pollinator/exploiter and plant/pollinator/florivore simulation models and their default values, chosen to be biologically reasonable

Parameter	Description	Default value
θ	Ovule production per season	.6
β	Mutualist visits per season	6
ε_E	Exploiter visits per season	
ε_F	Florivore visits per season	
γ	Mutualist oviposition probability	.5
δ_P	Plant mortality	.02
Δ_P	Maximum seed dispersal distance	2
Δ_M	Maximum mutualist dispersal distance	10
Δ_E	Maximum exploiter dispersal distance	
Δ_F	Maximum florivore dispersal distance	
	Lattice size	20 × 2,000

Pollinator Visits

After florivores attack flowers, adult females of the pollinator species visit sites, wherein they pollinate flowers and deposit their eggs. The average number of sites an individual pollinator visits during a single season is given by β. As for the florivores, the actual number of sites visited by an individual in any one time step is determined by a Poisson distribution. If a visited site is occupied by a plant, then the pollinator pollinates the plant's ovule (if present), regardless of prior pollination visits to that plant. That is, we do not incorporate in the model avoidance of previously visited flowers. Each pollinator visit involves two potential activities, pollination and oviposition. Both activities occur on every visit. However, only in a fraction γ of visits do the eggs survive to become larvae. On completion of a site visit, the pollinator disperses to a randomly selected site within distance Δ_M of its present site. In the end, any number of pollinators may oviposit into the same flower while its ovule is available for fertilization, but we assume that larval competition is so strong that at most a single pollinator offspring will mature per ovule. After all visits have taken place, adult pollinator insects die.

Exploiter Visits

On average, a single exploiter visits ε_E sites during its lifetime. Exploiter visits occur after all pollinator visits have been completed. Their interactions with the plants proceed in a similar manner as for pollinators, except that exploiters do not pollinate. Since exploiter larvae must consume seeds, oviposition by exploiters only occurs in flowers bearing ovules that have been fertilized by pollinators. Our previous models (Morris et al. 2003; Wilson et al. 2003) assumed that exploiter larvae were successful only if no mutualist larvae were present in the same fruit. We have reversed this competitive hierarchy in the present model to allow a more equitable comparison between exploiters and florivores: we now consider mutualist larvae to be successful only if no exploiter larvae are present in the same fruit. After completion of each site visit, the exploiter disperses to a new site chosen randomly from within distance Δ_E. After completion of all visits, adult exploiters die.

Reproductive Outcomes

Once all insect visits have been completed, a flower may contain florivore, pollinator, or exploiter larvae. If florivore larvae are present, one adult florivore emerges. If exploiter and pollinator larvae are present, one adult exploiter emerges. If pollinator larvae only are present, one adult pollinator emerges. Finally, if no larvae are present, then a seed is produced.

As stated previously, we are concerned with the comparison between two models, one including plants, pollinators, and florivores, the other including plants, pollinators, and exploiters. Our goal is to understand whether the two types of antagonists, exploiters and florivores, demonstrate any fundamental differences in their effects on the dynamics of mutualistic systems. We examine these two situations under nonspatial and spatial conditions. Both of these conditions use the identical simulation. However, in the nonspatial simulation, new offspring of all species are placed randomly over the entire habitat, independent of their parents' locations, and successive visits by insects occur anywhere in the habitat.

Results

Figure 2 depicts the temporal dynamics of the nonspatial simulation model of plants, pollinators, and antagonists, either exploiters (fig. 2*a*) or florivores (fig. 2*b*). We began each simulation with all three species at moderate densities. Every 500 simulation steps, we increased the average number of visits by the antagonist to explore the effect of the magnitude of antagonism on the dynamics of the system. The temporal dynamics indicate that as the number of per capita visits increases for either of the antagonists, the system's oscillatory dynamics become more extreme, finally leading to the extinction of one or more of the three species. Oscillations begin and extinction results at lower per capita visitation rates for florivores than for exploiters. For example, for the initial conditions represented in figure 2, florivores are driven to extinction when $\varepsilon_F = 2.5$, whereas exploiters are extinguished when $\varepsilon_E = 10.5$.

Across all runs of the model, which species go extinct in the end depends in part on the initial conditions. The conditions used in figure 2 result in extinction of the antagonist alone and allow plants and pollinators to persist. However, runs performed in a more traditional manner with the mutualists at their equilibrium densities (in the absence of antagonists) and a small inoculum of either exploiters or florivores can lead to the persistence of the three-species system, the extinction of the antagonists alone, or the extinction of all three species (results not shown; see also Morris et al. 2003). In these runs, as per capita visit numbers by antagonists increase, the likelihood first of extinction of antagonists alone, then of extinction of all three species, increases as well. In the plant/pollinator/florivore model, either florivores generally coexisted with the mutualists or all three species were driven extinct; in contrast, in the plant/pollinator/exploiter model, there was a wide region of parameter space in which exploiters alone went extinct.

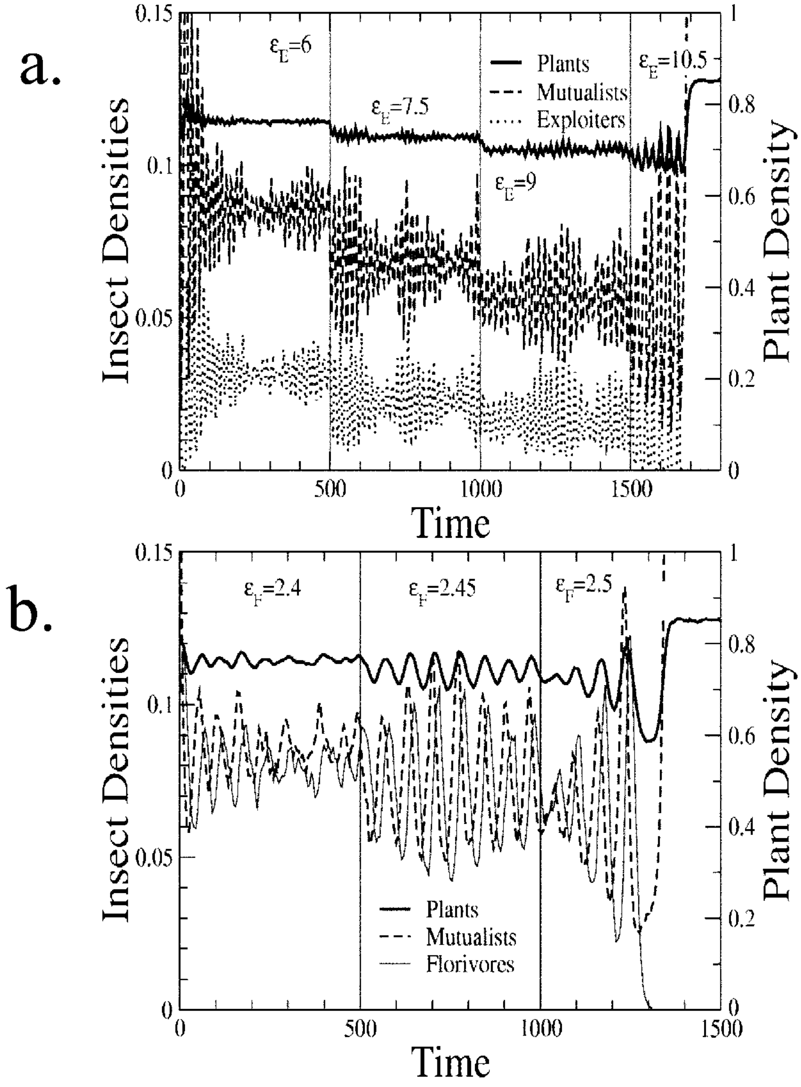

Figure 2: Temporal dynamics of (*a*) exploiter and (*b*) florivore systems in which all species show unlimited dispersal. Every 500 seasons or simulation steps, the average number of antagonist (i.e., exploiter or florivore) visits is changed to the indicated value (ε_E or ε_F, respectively). Initial densities are 0.8 for the plants, 0.3 for the mutualists, and 0.1 for the exploiters and florivores. Both systems demonstrate increasing oscillations as the number of antagonist visits is increased, leading to the extinction of the antagonist but the persistence of the mutualism.

Results of the nonspatial simulation runs displayed in figure 2 are shown in an alternative format in figure 3. Taking a transect across the 20 × 2,000-site lattice, we plot occupied cells as dark pixels. Each horizontal line of pixels represents the occupancy states of this transect; appending subsequent time steps vertically leads to a two-dimensional figure representing the spatiotemporal dynamics of the system. To account for low antagonist density, we plot a dark pixel if any site within the 20 rows in a given column are occupied. In both figure 3*a* (the plant/pollinator/exploiter system) and 3*b* (the plant/pollinator/florivore system), the dynamics are relatively stable at lower visitation rates, then destabilize (i.e., become more oscillatory) at higher values. For example, at $\varepsilon_E = 9$ in figure 3*a*, striated bands in the insect densities reveal alternating times of low and high population densities; these are the identical oscillatory dynamics depicted at the same parameter value in figure 2*a*, but figure 3*a* shows that these oscillations are synchronized across space. Finally, at the highest visitation rates shown in figure 3, the antagonist species go extinct, reflecting the extinctions in figure 2. We also see the two mutualistic species attaining their equilibrium densities after the antagonists perish.

Figure 4 shows the results for spatial simulations of the

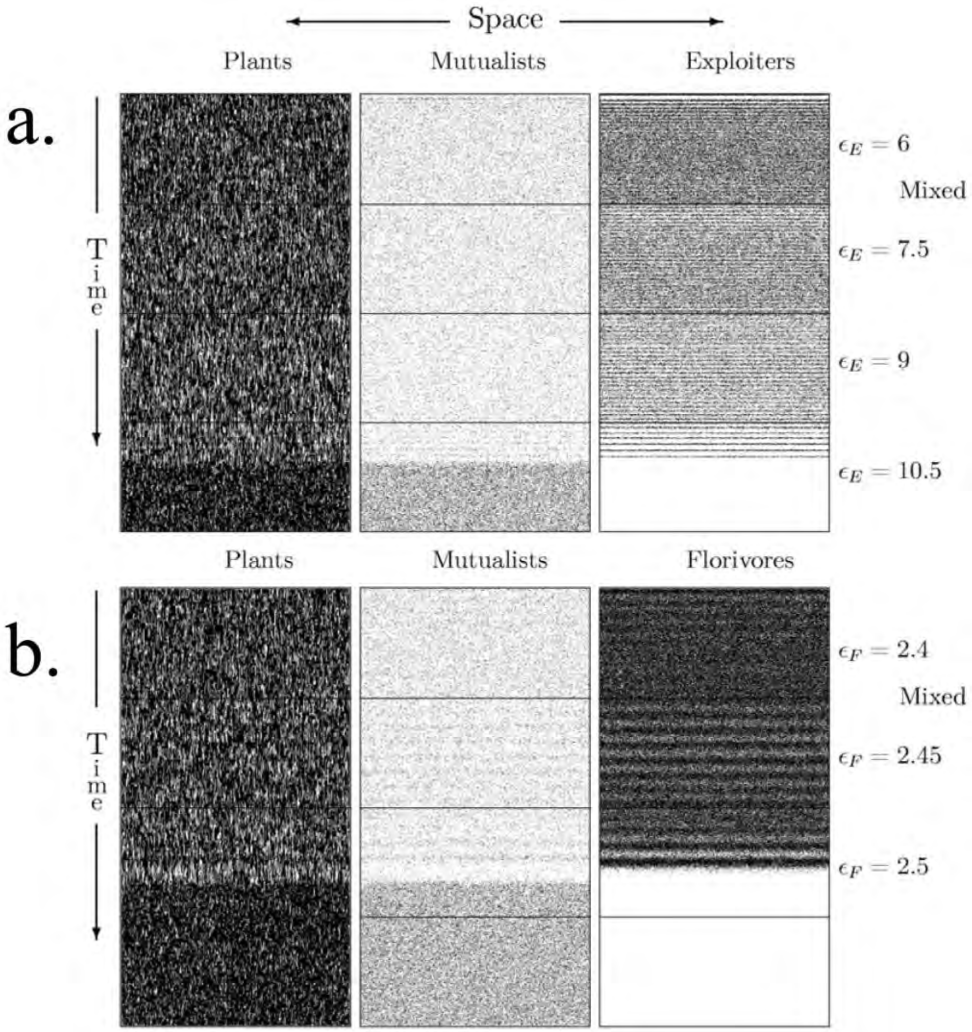

Figure 3: Space-time images from the nonspatial simulation runs presented in figure 2. A lattice of size 20 × 2,000 sites is used with an algorithm that ensures spatial homogeneity in densities. Dark pixels for plants and mutualists represent occupied sites along one lattice row. Every fourth pixel is plotted each time step. For exploiters and florivores, a dark pixel represents occupancy in any of the 20 rows to enhance visual clarity. Oscillations are evident from the horizontal bands that indicate high occupancy of cells at a specific instant in time.

plant/pollinator/exploiter model for three different exploiter dispersal distances as well as at a range of average per capita exploiter visitation numbers. Figure 5 shows parallel results for the spatial simulations of plants, pollinators, and florivores. The same general features hold in both cases. In contrast to the situation in figure 3, in which the three species were always dispersed uniformly across the lattice, figures 4 and 5 involve limited dispersal of two or more species, which allows spatial correlations to develop. Note the following features. First, in both the exploiter (fig. 4) and florivore (fig. 5) model, spatial structure emerges during the first 500 steps of each simulation, leading to alternating patches of high and low species densities. For example, at $\Delta_E = 20$ and approaching $\varepsilon_E = 8$ in figure 4*a*, densities of all three species have gone to 0 by time 500 in about half the sites but are still above 0 in the other half. Second, spatial patterning erupts at relatively low numbers of per capita antagonist visits and persists as per capita visits increase. This result is consistent with similar modeling results that indicate stable pattern formation in simulation models of activator-inhibitor systems such as host-parasite, predator-prey, and mutualist-exploiter models (Wilson 1998); it is discussed in detail by Wilson et al. (2003). Third, antagonists alone go extinct at relatively low visitation numbers when they have low dispersal distances, leaving the plants and pollinators persisting in their

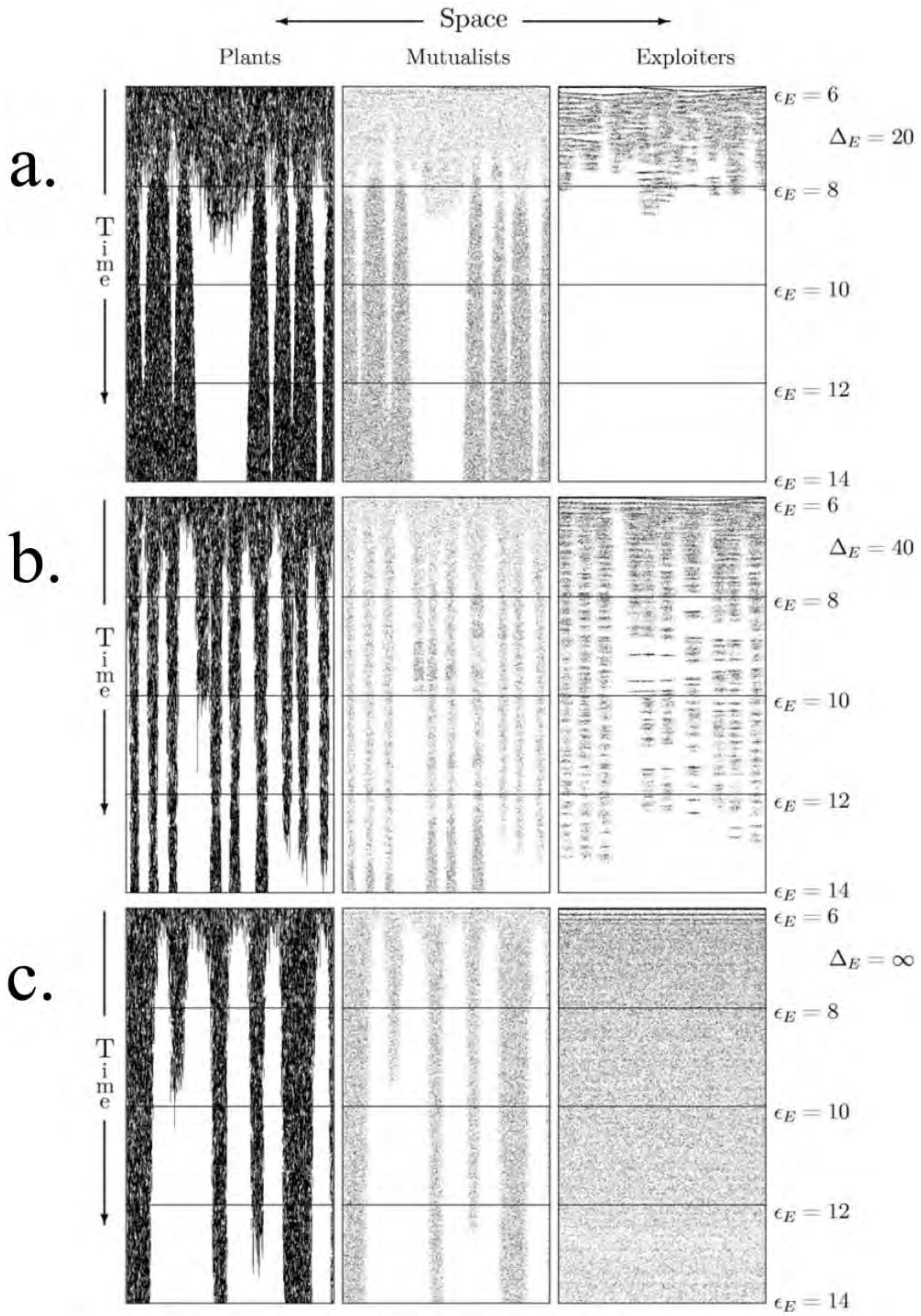

Figure 4: Spatial dynamics of the mutualism-exploiter system at three exploiter dispersal distances. Duration of each run is 2,000 seasons; horizontal lines demarcate intervals of 500 seasons. Every 100 seasons, ε_E (the average number of exploiter visits) is increased by 0.4. In this spatial model, all participants in the interaction show restricted dispersal: seeds disperse two sites from the parent, and mutualists move 10 sites between each plant visit. Only the left half of the lattice is initialized with exploiters in order to generate initial spatial heterogeneity. *a*, Relatively low exploiter dispersal results in small-scale patchiness, and the small isolated populations that result lead to exploiter extinction at relatively low visitation numbers. *b*, Increased exploiter dispersal enhances spatial pattern formation and also permits exploiters to recolonize patches where they have gone locally extinct, leading to exploiter persistence at higher visitation numbers. *c*, A well-mixed exploiter population (i.e., very high dispersal) promotes fixed spatial patterning in the mutualism and temporal stability in the exploiters.

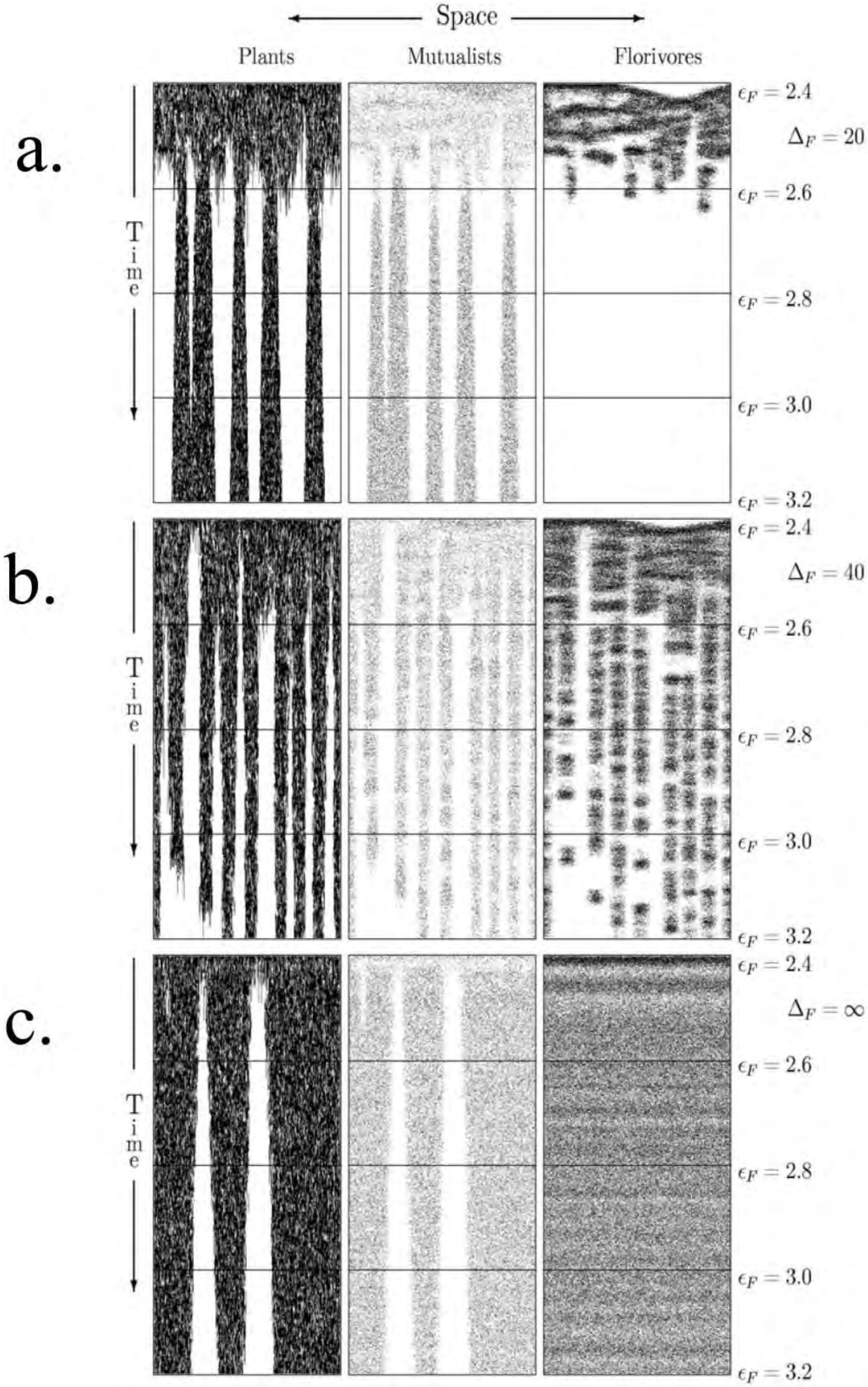

Figure 5: Spatial dynamics of the mutualism-florivore system under the same conditions as in figure 4. Every 100 seasons, ε_F is increased by 0.04 visits. *a*, Relatively low dispersal leads to florivore extinction at low visitation numbers. *b*, *c*, For higher florivore dispersal distances, florivore persistence is enhanced through spatial effects.

absence. Finally, as the antagonist dispersal distance increases, the system organizes into a collection of spatially fixed patches. At moderate dispersal distances, antagonists display outbreak dynamics, invading local patches occupied by plants and pollinators, attaining high densities, and then declining to local extinction while the mutualist pair persists (e.g., at $\Delta_E = 40$; fig. 4*b*); at yet higher dispersal distances, exploiters maintain constant density across space (e.g., at $\Delta_E = \infty$; fig. 4*c*). This fixed spatial patterning leads to the persistence of all three species at visit numbers that would lead to extinction in the nonspatial case.

Discussion

Mutualisms clearly are not isolated from the communities in which they occur. Yet, empirical and theoretical studies of pairwise mutualisms have proliferated, in large part because of their relative ease of study. Stanton (2003) has pointed out that these studies now form the basis of the somewhat inaccurate view of mutualism heavily represented in current textbooks. At the same time, however, it should be acknowledged that this body of research has been essential in revealing the kinds of selection pressures and constraints that potentially shape the ecology and evolution of mutualisms. The challenge now is to place these mutualisms back into their appropriate community contexts in order to clarify how they actually might function in nature.

A reasonable jumping-off point for tackling this challenge is to explore how the ecological dynamics of well-understood, obligate, species-specific mutualisms are affected by the presence of other species that interact strongly with them. Pollinating seed parasite mutualisms are obvious choices for such an endeavor. These are among the most specialized plant/animal mutualisms known, and they are probably the most thoroughly studied from the pairwise perspective. Yet they do not function in isolation from other species in their communities. More and more cases are being recognized in which alternative partner species are available for one or both mutualists (e.g., Kerdelhué et al. 1999; Pellmyr 1999; Després et al. 2002). In addition, these mutualisms tend to attract species able to obtain the goods and services the mutualists offer each other while offering nothing in return. Many of these antagonistic species are nearly as specialized as the mutualists themselves. It is therefore feasible to study theoretically how these mutualisms function in the presence of other species without the system being so large as to be analytically intractable.

Obligate Mutualisms Can Persist in the Presence of Obligate Antagonists

Mutualisms have commonly been perceived to be fundamentally unstable interactions, from both a population dynamics and an evolutionary viewpoint. The positive feedback inherent to mutualisms led May (1976, p. 66) to characterize mutualisms as "an orgy of mutual benefaction." A newer generation of population models, however, has shown that mutualisms are stabilized whenever benefits of the mutualism to one species first increase but then saturate or decrease with increasing abundance of its partner (Boucher 1985; Holland et al. 2002; Morris et al. 2003). Antagonistic species that limit population sizes of the mutualists have been proposed to have precisely this effect (e.g., Heithaus et al. 1980), suggesting that they could alter the dynamics of mutualism in such a way as to stabilize these interactions. In contrast, many biologists have perceived antagonism (under a variety of names, including cheating, exploitation, predation, or parasitism) to threaten the ecological and evolutionary persistence of mutualisms. In this view, antagonists have the advantage of benefiting from the mutualists while paying none of the costs inherent to reciprocation. Adaptations have therefore been sought by which antagonists could be kept under control (e.g., Yu 2001; Johnstone and Bshary 2002; West et al. 2002). Thus, antagonistic species have been well recognized to potentially affect the dynamics of pairwise mutualisms, but there has been little agreement as to whether these effects tend to threaten or to bolster the stability of the mutualism.

The net effects of mutualism to plants associated with pollinating seed parasites first increase, then decrease with increasing pollinator numbers. At low pollinator numbers, the benefits of pollination outweigh the costs of seed consumption by pollinator offspring, whereas at higher pollinator numbers, the costs outweigh the benefits (Bronstein 2001*a*). This unimodal relationship between plant reproduction and pollinator abundance can stabilize the population dynamics of these pairwise mutualisms (Holland and DeAngelis 2001; Holland et al. 2002; Morris et al. 2003). More specifically, these mutualisms proceed to one of two stable points, either extinction of both species or stable, joint persistence, depending on whether the initial densities of the two mutualists are below or above a threshold (i.e., there is an Allee effect; see, e.g., Groom 1998; Lundberg and Ingvarsson 1998). Adding an antagonist species that reduces mutualist success could therefore be expected to have a wide range of effects on the dynamics of these mutualisms, depending on how much they depress population sizes.

Our models demonstrate that pollinating seed parasite mutualisms have the ability to persist in the presence of at least two antagonist types over a relatively wide range of antagonist densities and life-history traits. In nonspatial models under a range of initial conditions, they can persist in association with nonpollinating seed parasites (exploiters) that compete with pollinator larvae for the seeds fertilized by the pollinators. This is the case whether the competitive advantage is experienced by the exploiters (models presented here) or by the pollinators (Morris et al. 2003; Wilson et al. 2003) and for a wide range of exploiter visitation frequencies (figs. 2*a*, 3*a*; W. G. Wilson, unpublished data). Note that we have assumed severe competition between pollinators and antagonists. Less severe competition should only make coexistence easier to achieve. Results of spatially explicit models in turn show that mutualists are able to persist in at least a subset of patches over a wide range of exploiter dispersal distances (fig. 4*a*). These mutualisms persisted nearly as well in the presence of florivores (figs. 2*b*, 3*b*, 5), antagonists whose negative impact is quantitatively rather different from that of the exploiters. The stable spatial patterns that underlie persistence arise by an activator-inhibitor mechanism (Murray 1989). This mechanism requires that antagonists disperse further than mutualists, which results in the greater loss of antagonists to the intervening space once patches of mutualists have formed (Wilson et al. 2003).

In addition to assuming that the mutualist is competitively inferior to the exploiter, the models of plant/pollinator/exploiter dynamics presented here differ in another important respect from those of Wilson et al. (2003). In both cases, we incorporated a strong asymmetry of life spans between plants and their pollinating seed parasites. However, in Wilson et al. (2003), we simulated insects whose life span was five seasons, whereas here they live only a single season. More work needs to be done to fully understand the differences induced by this change, but it seems that when insect longevity is shorter, the mutualism is more resilient in the presence of exploiters over a wider range of parameter space. Evidently, longer-lived exploiters reduce mutualist densities progressively across seasons, adding up to a more negative impact; when exploiters live only a single year, overexploitation leads exploiter populations to crash, after which the longer-lived plants can recover (provided that pollinators have survived). This unexpected importance of relative generation times is particularly intriguing, since across obligate mutualistic systems differing widely in natural history, partners typically exhibit highly divergent generation times. In pollinating seed parasite mutualisms, for example, pollinators typically live no longer than a few days as adults (e.g., Bronstein 1992), whereas the plants they pollinate are all perennials.

Although both exploiters and florivores can coexist with plant-pollinating seed parasite mutualisms without driving them extinct, they may alter the dynamics of those mutualisms. Using deterministic, nonspatial models, we have shown that the two-species plant-pollinator system is apparently always stable (Morris et al. 2003). However, as seen most clearly in figure 2, the presence of antagonists can induce dramatic population fluctuations in the mutualist populations, particularly when all three species disperse their offspring broadly. Furthermore, their presence can lead to the emergence of significant spatial structure in the plant-pollinator association, particularly when the antagonists exhibit high per capita visitation frequencies and long dispersal distances relative to the mutualists (figs. 4, 5; see also Wilson et al. 2003).

In nature, many pollinating seed parasite mutualisms have in fact been noted to exhibit large population fluctuations of one or both partners as well as spatially patchy distributions (e.g., Bronstein and Hossaert-McKey 1996; but see Addicott 1998). These features characterize many other types of mutualism as well (Yu and Davidson 1997; Herrera 1998; Parker 1999). We would not go so far as to claim that this type of spatiotemporal variation is attributable to the actions of antagonistic species, as seen in our relatively simplified models. However, in light of the theme of this symposium, it is worth pointing out that these phenomena emerge in our models only when we place pairwise mutualisms into a minimally more complex community context. We are unaware of any strictly pairwise model of mutualism that produces the range of spatial and temporal dynamics that emerge within our mutualist/antagonist models or within two other, recent models in which mutualists interact with a third species (Yu et al. 2001; Bacher and Friedli 2002).

Obligate Antagonists Persist Poorly

Although mutualists persisted relatively well in the presence of antagonists (at least in a subset of patches in the habitat), the converse was not equally true. Most strikingly, in the spatial version of the model, antagonists consistently went to extinction when their dispersal distances and per capita visitation frequencies were both low (figs. 4*a*, 5*a*). They were able to persist over the entire habitat only when their dispersal distances were set unrealistically high (figs. 4*c*, 5*c*). At moderate dispersal distances, antagonists persisted in only a subset of the patches of mutualists that their activities created.

As stated previously, it is commonly assumed that highly specialized antagonists pose a particular threat to the evolutionary persistence of mutualisms, such that mechanisms must exist to keep their numbers or effects low. However, dynamics such as those found in our models point to the fundamental difficulty inherent to a life history that is based on species-specific exploitation of an interaction. As these antagonists increase in numbers, the numbers of one or both mutualists on whom they depend drop, limiting their own success. Antagonists can only persist if mutualist numbers are able to rebound sufficiently quickly or else if antagonists can disperse to patches where mutualists are still abundant.

Exploiters of pollinating seed parasite mutualisms apparently have been associated with these interactions for most of the evolutionary history of those mutualisms (Desprès and Jaeger 1999; Pellmyr and Leebens-Mack 1999; Lopez-Vaamonde et al. 2001). This observation implies the existence of exploiter traits that favor both their own persistence and that of the mutualism with which they associate. The results of our models suggest that one critical life-history trait is the ability to disperse long distances in search of new patches of mutualists. Although no direct information on flight distances is currently available, nonpollinating seed parasites are generally both larger and longer-lived than the pollinating seed parasites with which they are associated (Compton et al. 1994; Jaeger 1998; O. Pellmyr, personal communication), making greater flight capabilities rather likely. Longer flight distances are also expected since the exploiters must locate a lower density resource, even in a fairly uniform habitat: they oviposit within developing fruits, which will be consistently rarer than the flowers for which the pollinators search (fruit set is often quite low in these plants; Bronstein 2001*a*). Unfortunately, very little is currently known about the specialized florivores associated with these mutualisms. Once available, these data will provide a valuable test of whether generalizations with regard to natural history comparisons between closely related pollinating and nonpollinating seed parasites apply to a quite different kind of antagonist.

Our models pertain to antagonists that associate exclusively with a single pair of mutualists, which are themselves obligate associates. Specialists are often treated as the only associates who can break the code (Letourneau 1990) of obligate mutualisms and exploit them successfully. In pollinating seed parasite mutualisms, specificity has been assumed to be essential both for locating mutualists to exploit (e.g., in figs, by the use of species-specific plant volatiles; Gibernau and Hossaert-McKey 1998) and for ovipositing within highly modified reproductive structures (e.g., in figs, having ovipositors of sufficient length to access oviposition sites; Weiblen and Bush 2002). However, extreme species specificity, while certainly well documented, may ultimately prove to be the exception rather than the rule among antagonists of these mutualisms. Indeed, there is growing evidence that the nonpollinating seed parasites of many yuccas (Pellmyr 1999, 2003) and figs (Weiblen et al. 2001) are associated with more than one mutualist pair, although the spatial scale of this lack of specificity (i.e., whether it occurs within or between populations) has been minimally explored to date. Any antagonist able to shift to exploiting a new association when its current hosts become locally rare should enjoy an added protection against extinction. It should also be able to inflict considerably more negative effects on the mutualists without experiencing the kind of self-limiting feedback we document in the present models. Hence, we predict that facultative exploiters of mutualisms should inflict considerably stronger effects on any one mutualism than will obligate exploiters.

Are All Antagonists Equal?

Although the community context can radically alter the outcome of pairwise species interactions, entire suites of species may interact in qualitatively similar ways with one or both of the species involved in a focal interaction. For example, one species involved in the focal interaction may have several different species of predator or parasite, all of which increase its deathrate or decrease its birthrate, albeit to quantitatively different degrees. Thus, a key question in understanding the importance of the community context for the outcome of mutualisms is how much we can generalize about the effects of antagonist species that differ somewhat in natural history. This is a particularly important question in light of the unique threat that exploiters are thought to pose for the evolutionary persistence of mutualisms. In a population dynamics sense, are specialized exploiters of mutualism really any different from other kinds of antagonists?

In the models presented here, we contrasted the dynamics of pollinating seed parasite mutualisms associated with exploiters (nonpollinating seed parasites that compete for seeds within fertilized flowers) versus florivores (species that feed on flowers before the pollinators and exploiters can use them). Evolutionarily, these two kinds of antagonists differ substantially. Many exploiters are "mutualists one step removed"; that is, they have evolved from mutualists through the loss of reciprocation at some point in their evolutionary history (Desprès and Jaeger 1999; Pellmyr and Leebens-Mack 2000). In contrast, most other antagonists are only distantly related to the pollinators. For example, the major florivores attacking figs and yuccas are beetles and flies, whereas the pollinators are wasps and moths, respectively. They differ ecologically as well. Perhaps most importantly, exploiters can reproduce successfully only within patches where both plants and pollinators have colonized, whereas florivores can persist even when pollinators are absent. Thus, these two kinds of antagonists might be expected to inflict highly contrasting impacts on their host mutualisms.

In fact, we found surprisingly little difference between the ecological effects of florivores and exploiters, with the few identifiable differences being quantitative rather than qualitative in nature. In general, florivores tended to drive themselves (and sometimes the mutualists) to extinction at parameter values at which the exploiters were able to persist. For example, florivores induced oscillatory dynamics in the mutualists at lower per capita visitation frequencies than did the exploiters. Furthermore, when one or more of the three species were driven to extinction, this occurred at lower per capita visitation frequencies (e.g., cf. fig. 2*a* and 2*b*). This may be because the florivores' lack of reliance on the presence of pollinators (in the short term) means that a greater proportion of their visits will result in a successful oviposition event. Alternatively (or perhaps additionally), because they can exploit flowers even in the absence of pollinators, florivores induce wider fluctuations at lower visit rates than do exploiters and then crash due to demographic stochasticity during the troughs of the fluctuations. We are currently exploring the relative importance of these two processes.

Thus, in our simulations, plant/pollinator/florivore communities tended to persist poorly compared with plant/pollinator/exploiter communities. In this light, it is interesting to note that while all well-studied pollinating seed parasite mutualisms are associated with at least one and often several species of nonpollinating exploiter, obligate florivores have been reported much more rarely (Udovic 1986; Huth and Pellmyr 1997).

Conclusions

Our models imply that mutualisms can persist surprisingly well in the presence of antagonists but that the presence of antagonists leads mutualisms to exhibit distinctly different temporal and spatial dynamics. These results suggest at least three clear lines for future research. First, theoretical studies need to be directed toward understanding the persistence of mutualisms exhibiting a broader range of natural histories than the quite specialized one modeled here. In particular, remarkably few predictions exist about factors promoting the ecological and evolutionary persistence of facultative rather than obligate mutualisms (but see Law and Koptur 1986), even though the majority of mutualisms in nature are in fact facultative and relatively generalized. Second, further empirical studies of antagonist species and how they affect the costs and benefits of mutualism are clearly needed. In the case of the well-studied pollinating seed parasite mutualisms, much information is already available on the natural history, evolution, and phylogenetics of their common associates (e.g., Compton et al. 1994; Huth and Pellmyr 1997; Pellmyr and Leebens-Mack 2000; Lopez-Vaamonde et al. 2001). Unfortunately, little of the information currently available is helpful for evaluating the predictions of our models, for instance, with regard to relative dispersal distances and fecundities of pollinators and exploiters. Even more important are field studies of how other kinds of mutualisms function in the presence of antagonists. Particularly promising work in this area is being conducted on obligate ant/plant defensive mutualisms, which are commonly afflicted with ants that fail to protect the plants (Gaume and McKey 1999; Yu et al. 2001). Evidence for competition/colonization trade-offs in these interactions (reviewed by Palmer et al. 2003) is consistent with some of the predictions of our models, particularly with regard to the importance of long-distance dispersal of exploiters as a factor facilitating mutualist/exploiter coexistence.

Finally, it is obviously essential to extend the community perspective on mutualisms beyond the three-species perspective we adopted here. It could be argued that adding a single additional species to a pairwise mutualism does not elevate this work much beyond what a pairwise perspective might provide. In response, we point to the fact that the ecological dynamics of the mutualisms we have modeled clearly become much more complex—and much more interesting—when even one more species is added. (See Gomulkiewicz et al. 2003 for a similar observation at the evolutionary timescale.) Furthermore, we have provided evidence that pairwise mutualisms can in fact persist ecologically in the presence of specialized and abundant antagonists, a point that has been subject to some dispute in recent years. These interactions therefore have the potential to serve as a template for the accumulation of yet more species within biological communities.

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