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Interactions among interactions: The dynamical consequences of antagonism between mutualists

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ABSTRACT

Species often interact with multiple mutualistic partners that provide functionally different benefits and/or that interact with different life-history stages. These functionally different partners, however, may also interact directly with one another in other ways, indirectly altering net outcomes and persistence of the mutualistic system as a whole. We present a population dynamical model of a three-species system involving antagonism between species sharing a mutualist partner species with two explicit life stages. We find that, regardless of whether the antagonism is predatory or non-consumptive, persistence of the shared mutualist is possible only under a restrictive set of conditions. As the rate of antagonism between the species sharing the mutualist increases, indirect rather than direct interactions increasingly determine species' densities and sometimes result in complex, oscillatory dynamics for all species. Surprisingly, persistence of the mutualistic system is particularly dependent upon the degree to which each of the two mutualistic interactions is specialized. Our work investigates a novel mechanism by which changing ecological conditions can lead to extinction of mutualist partners and provides testable predictions regarding the interactive roles of mutualism and antagonism in net outcomes for species' densities.

1. Introduction

The vast majority of species on Earth interact with multiple mutualists (Stanton, 2003). Plants, for example, commonly interact with both biotic pollinators and biotic seed dispersers; similarly, aphids can interact with both mutualistic gut endosymbionts and ants that defend them from natural enemies. The presence of one mutualism can impact the strength or outcome of another, such that the net effect of these simultaneous interactions on the shared mutualistic species can be positive or negative and can range from sub-additive to synergistic (Afkhami et al., 2014). Even the net outcome of a single pairwise mutualism is often contingent upon factors that vary with ecological context (Chamberlain et al., 2014; Hoeksema and Bruna, 2015). Systems involving multiple simultaneous mutualisms should be even more complex, as the net outcome for each pairwise mutualistic interaction will also be influenced by interactions among the other species in the system. While competition for partners or rewards within and between mutualists has been addressed in theoretical and empirical studies (reviewed in Jones et al., 2012; Johnson and Bronstein, 2019), partners may also interact directly and antagonistically (Afkhami et al., 2014), such as when ants attack the pollinators of plants they defend from herbivores (Ness, 2006). Here, we explore how antagonism between species sharing a mutualist influences the population dynamics of the entire mutualistic system.

When species have a direct antagonistic interaction (e.g., one consumes the other), mutualistic partners that they share will experience complex indirect effects that will influence their ecological and evolutionary trajectories (terHorst et al., 2018). Despite their inherent time lag, indirect interactions that occur when individuals of one species affect another species' density through a third species are often of comparable magnitude to direct interactions such as predation (Wootton, 1994a,b). Therefore, even

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predicting whether an increase in the density of one species (e.g., a press perturbation) will increase or decrease the density of another can be impossible when only direct interactions between the two species are considered (Yodzis, 1988). Several phenomena that have received considerable attention in community ecology (e.g., keystone predation, apparent mutualism, apparent competition) are indirect interactions resulting solely from negative direct interactions (Menge, 1995, Abrams et al., 1998). In such systems, understanding indirect effects is critical to predicting species' responses to change. As communities invariably include both positive and negative interactions, there is also a need for studies of the ecological consequences of indirect effects in systems of coupled mutualism and antagonism.

The need for general theory that can qualitatively predict how species will respond to complex "interactions among interactions" has recently been emphasized (terHorst et al., 2018). Previous theoretical work has focused almost exclusively on either mutualistic or antagonistic interactions alone (but see Yoshikawa and Isagi, 2013; Georgelin and Loeuille, 2013; Suave et al., 2014; Genrich et al., 2017; Luo et al., 2018), despite knowledge that inclusion of different interaction types will influence network structure and stability (Melián et al., 2009; Fontaine et al., 2011; Mougi and Kondoh, 2012; Pillai et al., 2014, Suweis et al., 2014, Bachelot et al., 2015). While pivotal, these prior theoretical works have focused on identifying network or metacommunity level consequences of communities of both mutualists and antagonists rather than isolating the effects of individual direct and indirect effects on population dynamical outcomes. The use of simple mechanistic models has led to significant insights into how mutualisms can be stable when faced with exploitation, competition, and cheating between small networks of interacting partners (Ferriere et al., 2002; Morris, Bronstein and Wilson, 2003; Ferrière et al., 2007; Jones et al., 2009; Lee and Inouye, 2010; Wang et al., 2019) or partners that interact positively or negatively depending upon their life stage (Ke and Nakazawa, 2018; Picot et al., 2019). However, this approach has rarely been used to examine the persistence of mutualism in the presence of other forms of antagonism, such as that between different mutualists providing non-overlapping benefits to their shared partner (but see Oña and Lachmann, 2011; Wang et al., 2014). In order to explore the consequences of antagonisms between functionally distinct mutualists, we develop a model describing the dynamics of systems involving coupled mutualism and antagonism, focusing on two species that may interact antagonistically and their shared mutualist species.

Antagonistic interactions between species that share a mutualistic partner are likely to have important consequences for the whole system, as negative indirect effects on the shared species could undermine the mutualistic effects. Thus, we develop a model to understand whether these antagonistic interactions are sufficient to cause extinction in mutualistic systems and might therefore help explain the apparent paucity of direct antagonism between species sharing mutualists in nature. An understanding of the effects of antagonistic interactions among mutualists on species' persistence is necessary, as anthropogenic changes to mutualistic networks are likely to provide new opportunities for these interactions. For example, introduced species (Lach, 2003) and climate change induced phenological shifts (Miller-Struttmann et al., 2015) are altering co-evolved mutualistic systems in ways that will potentially allow for new antagonisms to arise.

Here we use plant-pollinator-disperser systems to illustrate antagonisms between species sharing mutualistic partners. Plants often rely on animals for both pollination and dispersal (Howe and Smallwood, 1982; Traveset et al., 2007; Ollerton et al., 2011). Predators of pollinators are known to have strong indirect negative effects on plant reproductive success (Meehan et al., 2005; Knight et al., 2006; Romero et al., 2011; Gillespie and Adler, 2013). The population dynamical consequences of this predation on pollinators is likely to be particularly complex when perpetrated by frugivorous seed dispersers. Common seed dispersers include mammals, birds, and lizards, none of which can sustain themselves on a diet consisting solely of fruit, especially during breeding (Morton, 1973; Walsberg, 1977; Moermond and Denslow, 1985; Wheelwright, 1986; Olesen and Valido, 2003; Pérez-Mellado et al., 2006; Krauss et al., 2009; Bain et al., 2014; Orr et al., 2016). Therefore, most seed dispersers have an omnivorous diet, with many of them relying on insect prey (Levey and Martínez del Rio, 2001). If plants attract both insect pollinators and omnivorous vertebrate dispersers at overlapping times, some pollinators are likely to be consumed, at least incidentally. While likely of importance to animal pollinated and dispersed plants, such interactions are difficult to study and as a consequence their frequency in nature is not known.

We suggest that the biology of desert mistletoe (*Phoradendron californicum*), may be well-described by this model. This dioecious parasitic plant obligately relies on small generalist insect pollinators for seed producton and a specialist seed-dispersing bird, *Phainopepla nitens* (Larson, 1996), which in turn requires insects to supplement its diet (Walsberg, 1978; Miyoko and Walsberg, 1999). These silky flycatchers (Ptiliogonatidae) are unusual among primarily frugivorous species at being adept at catching flying insects; indeed, they spend up to 15% of their time engaging in flycatching during the breeding season (Walsberg, 1978). The flowering phenology of desert mistletoe overlaps completely with both its fruiting phenology and the phainopepla breeding period (Yule and Bronstein, 2018a). Guarded by territorial dispersers, flowering mistletoes are highly aggregated within host individuals and attract large numbers of pollinating insects (Yule and Bronstein, 2018b). Therefore, predation of pollinators by seed-dispersing phainopepla is likely to occur.

Seed dispersers need not consume pollinators, in this or other systems, to negatively affect the pollination interaction, however. When pollination is limiting for fruit production, increased densities of potential predators of pollinators can have negative indirect effects on plant female fitness even when predation *per se* is rare. These non-consumptive or trait-mediated indirect effects of predator presence can alter pollinator foraging behavior, leading to reduced visitation rates and visit durations to rewarding flowers (Jones, 2010). For example, pollinators sometimes limit their foraging in potentially risky areas in response to both visual and olfactory cues, even in the absence of any previous attacks in that location (Bray and Nieh, 2014). These shifts in foraging behavior could directly reduce pollination rates and plant fitness. Alternatively, when pollinators move more quickly among flowers due to the perception of predation risk, they may consume fewer floral rewards while still transferring sufficient pollen for plant reproduction (Altshuler, 1999).

The model that we employ is flexible enough to explicitly explore the direct and indirect responses of species to different types of antagonistic interactions (predatory vs. non-consumptive) between members of two species that interact mutualistically with different life-history stages of a shared partner. In addition, we use the model to compare the consequences of different levels of dependence of the two mutualist species on their shared mutualist. Specifically, we consider (a) a specialist disperser and pollinator; (b) a specialist disperser and a generalist pollinator; (c) a generalist disperser and a specialist pollinator; and (d) a generalist disperser and pollinator. With this model, we ask: 1) What are the population dynamical consequences of antagonism between members of functionally distinct mutualists for all species? 2) How do these dynamics change depending upon the type of antagonism (predatory vs. non-consumptive) and the dependence of the species on the mutualism (specialization vs.

generalism)? 3) How do the magnitude and direction of direct and indirect species interaction effects in this system change with the rate of antagonism? We predict that the shared mutualist will be increasingly susceptible to extinction due to negative indirect effects increasing with antagonistic interaction rates. Additionally, we predict that some of the negative indirect effects on the shared partner will be mitigated by generalism in the species being harmed. Finally, we predict that non-consumptive negative interactions will yield results similar to predation but allow for the persistence of the mutualistic system over a broader set of conditions.

2. Model

We consider a three-species community composed of two species that interact with different life-history stages of a shared mutualist species but are potentially engaged in a direct antagonism with each other. Here, a plant is the shared species. The plant population consists of two life-history stages, juveniles (seeds) and adults (mature plants), that interact with different mutualists. A pollinator interacts with adult plants and disperses gametes, thus increasing the plant's per capita reproduction, and a disperser interacts with seeds (by consuming fruits) to increase the plant's per capita establishment rate. The pollinator benefits in terms of increased per capita birth rate by consuming floral nectar, and the disperser benefits by consuming fruit. Pollinators and dispersers may be specialists or generalists depending on whether or not they also consume resources external to the mutualism. A novel feature of this model is that the two mutualists can also interact directly. We investigate three cases: dispersers do not interact directly with pollinators (0/0 interaction); dispersers prey upon pollinators (+/− interaction); and dispersers have a non-consumptive negative effect on pollinators (0/− interaction).

Consider a population of adult (i.e., mature) plants (M) that interacts with a pollinator (P) to produce seeds (S) that in turn mature after dispersal by a disperser (D). We assume that adult plants are limited by establishment sites, and all model variables and parameters are scaled such that the maximum adult plant density is one. The population dynamics of the three species are therefore described by the following system of differential equations:

$$\frac{dM}{dt} = e_M \alpha_{SD} SD(1 - M) - d_M M$$

$$\frac{dS}{dt} = e_{MP}\alpha_{MP} MP - e_{SD}\alpha_{SD} SD - d_S S$$

$$\frac{dP}{dt} = \alpha_P P + e_{PM}\alpha_{MP} PM + e_{PD}\alpha_{DP} PD - q_P P^2 - d_P P$$

$$\frac{dD}{dt} = \alpha_D D + e_{DS}\alpha_{SD} DS + e_{DP}\alpha_{DP} DP - q_D D^2 - d_D D$$

where M and S represent the population densities of adult plants and seeds, respectively. P is the population density of the pollinator, and D is the population density of the seed disperser. Dispersers interact with seeds at a per capita rate ofα_{SD}. This interaction leads to removal of seeds with efficiency e_{SD} and conversion into disperser births with efficiencye_{DS}. Only a proportion, e_M, of these consumed seeds are dispersed successfully to suitable sites. Seeds are produced as an outcome of pollination with per capita rate, α_{MP}. This interaction results in the production of seeds with efficiency e_{MP} and conversion of floral nectar into pollinator births with efficiency e_{PM}. q_P and q_D quantify self-regulation in the pollinator and disperser populations, respectively, due to intraspecific interference competition, territoriality, or exploitative competition for resources external to the model. Each modeled population i suffers mortality at per capita rate d_i.

The novel interaction in this model occurs between pollinators and dispersers, which interact at per capita rate α_{DP}. The signs of the conversion efficiency parameters associated with this interaction, e_{DP}ande_{PD}, determine the type of interaction between these species. When pollinators and dispersers do not interact directly ($\alpha_{DP} = 0$), the model describes a shared plant with two mutualists that provide non-overlapping benefits (see *Results: No direct interaction between disperser and pollinator*). When the antagonism is predatory, it has a positive effect on dispersers and a negative effect on pollinators ($e_{DP} > 0, e_{PD} < 0$) (see, for example, *Results: Consumption of pollinators by dispersers*). In contrast, when the antagonism is non-consumptive, pollinators are negatively affected by increasing disperser densities, but dispersers do not benefit as a consequence ($e_{DP} = 0, e_{PD} < 0$) (see *Results: Non-consumptive negative effect on pollinators*). Table 1 shows the parameter combinations and figures depicting results for each of the scenarios we model here.

Finally, the model allows for different degrees of specialization in the disperser and pollinator. α_P and α_D are the per capita birth rates of pollinators and dispersers, respectively, due to consumption of external food sources assumed to be of constant density (Table 1). We define pollinator or disperser species i as having a generalist feeding strategy when $\alpha_i > 0$. We use the term specialist to denote $\alpha_i = 0$. It is important to note that we term dispersers "specialists" when $\alpha_D = 0$, even though they can still consume both insects and fruit when $e_{DP}\alpha_{DP}$ and $e_{SD}\alpha_{SD}$ are both greater than zero.

While the majority of mutualistic interactions are facultative in nature because species can typically persist in the absence of a given mutualist partner (Howe, 1984), we focus on the case in which the plant obligately depends upon both mutualists. Additionally, for simplicity, the model assumes that all resources are substitutable (e.g., dispersers need not consume both insects and fruits to persist). This scenario likely represents the worst case for persistence of the shared plant, so it is of most interest for understanding how indirect effects of antagonism can affect the persistence of the shared mutualist partner. However, preliminary, numerical analyses of the population dynamics resulting from modifications to the model that allow for (1) facultative, rather than obligate, mutualisms for the plant or (2) non-substitutable resources for the disperser yield qualitatively similar results to those we present here (see Supplementary Material S1).

All species interactions in the model are described by linear functions for simplicity. Importantly, self-limitation in each species prevents unbounded population growth due to ever-increasing benefits from mutualism (Holland et al., 2002), precluding the need for more complex saturating functions strictly to ensure bounded growth. The value of linear functional responses is that they enable us to better isolate the joint effect of antagonism and mutualism on the dynamics of the system. As persistent oscillations do not occur in either mutualistic models or Lotka-Volterra predator-prey models with a linear Type I functional responses (Murdoch et al., 2003), we can deduce that persistent oscillations in the model are driven entirely by the interaction between mutualism and antagonism.

Although we do find analytical equilibria for the full system, these are too complex to readily provide insights and render further analytical analyses intractable (see Supplementary Material S2-3). Therefore, we perform two principal numerical analyses: (1) stability analysis of equilibria across parameter space and (2) quantification of the direct and indirect effects of each of the system's component interactions.

2.1. Stability analysis

We numerically assess the stability of the positive equilibria for which all species persist ($\mathrm{M}^*, \mathrm{S}^*, \mathrm{P}^*, \mathrm{D}^* > 0$) using standard

Table 1
Modeled scenarios with corresponding parameter values and figures depicting associated results.

Interaction	Consumptive	Pollinator	Disperser	α_{DP}	e_{DP}	α_P	α_D	Results figures
None	NA	Generalist	Generalist	0	NA	>0	>0	A1
			Specialist	0	NA	>0	0	A2
		Specialist	Generalist	0	NA	0	>0	A3
			Specialist	0	NA	0	0	A4
Antagonism	Yes	Generalist	Generalist	>0	<0	>0	>0	1e-f, h-i
			Specialist	>0	<0	>0	0	1d, g; 2–4; A5-7
		Specialist	Generalist	>0	<0	0	>0	1b-c
			Specialist	>0	<0	0	0	1a
	No	Generalist	Generalist	>0	0	>0	>0	5e-f, h-i
			Specialist	>0	0	>0	0	5d, g
		Specialist	Generalist	>0	0	0	>0	5b-c
			Specialist	>0	0	0	0	5a

Routh-Hurwitz criteria for each of the feasible equilibria determined from the characteristic equation of the Jacobian matrix (May, 1973) (See Supplementary Material S2). We also consider the stability of positive equilibria for subsets of the community, ($P^* > 0$; $D^* > 0$; $P^*, D^* > 0$). Positive equilibria of the specialist shared plant in the absence of pollinators and dispersers are not possible (M^*, $S^* > 0$). We plot areas of parameter space for which the possible equilibria are stable (Figs. 1-2, 5, A1-4, A6).

For parameter values with no stable non-trivial equilibria, we inspect the population dynamics to check for persistent oscillations in species' densities. We identify regions of damped oscillations by determining areas of parameter space in which eigenvalues of the Jacobian matrix have non-zero imaginary parts and all negative real parts. Persistent oscillations around unstable equilibria are verified by phase-plane analysis (Fig. A5).

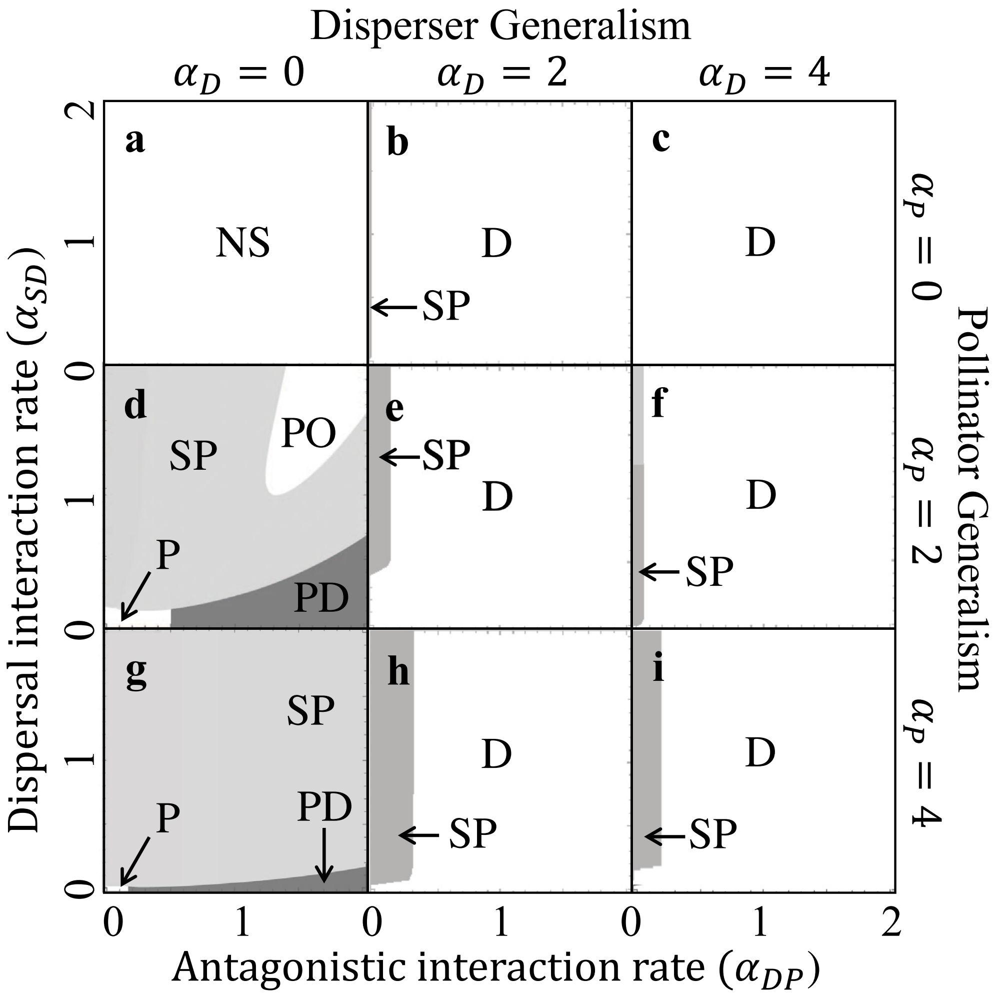

Fig. 1. Region plots depicting the population dynamical consequences of consumption of pollinators by dispersers as a function of dispersal (α_{SD}) and antagonistic (predatory) interaction rates (α_{DP}). The columns represent levels of diet specialization in the disperser with $\alpha_D = 0$ indicating full specialization on the modeled species and increasing values of α_D indicating increasing generalism or use of resources external to the model. The rows similarly represent levels of diet specialization in the pollinator. Dynamical outcomes are labeled as follows: NS indicates that no species persists, P is a pollinator-only community, D is a disperser-only community, PD is a predator-prey system consisting of only pollinators and dispersers, SP represents stable persistence of all species, and PO represents persistent oscillations in all species $\{e_M = 0.5, e_{MP} = 1, e_{SD} = 1, e_{PM} = 0.2, e_{DS} = 0.2, e_{DP} = 0.2, e_{PD} = -1, d_S = 1, d_P = 1, d_D = 1, d_M = 1, q_P = 0.1, q_D = 0.1, \alpha_{MP} = 4\}$.

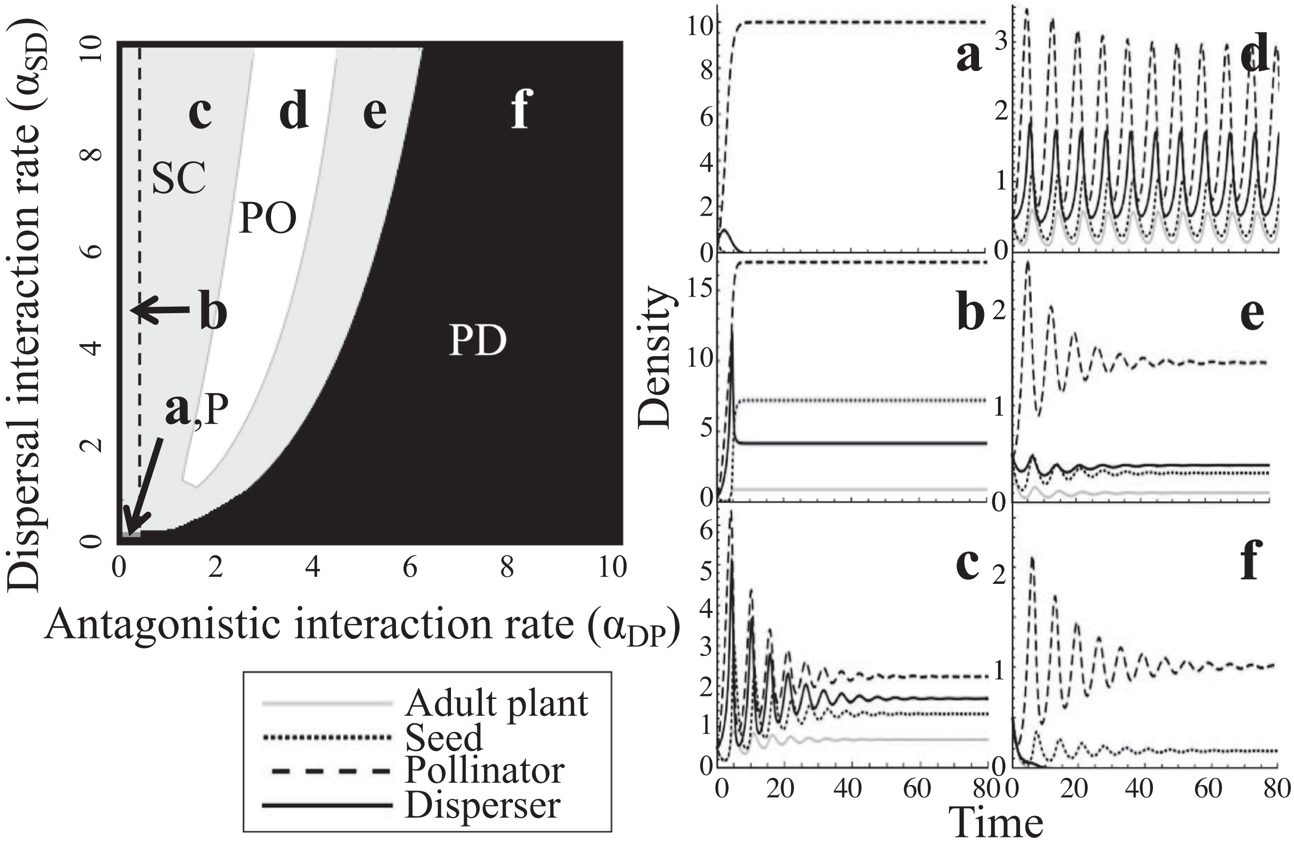

Fig. 2. Dynamical consequences of the three-species system as a function of the dispersal (α_{SD}) and consumptive, antagonistic (α_{DP}) interaction rates when the pollinator is a generalist and the disperser is a specialist (Fig. 1d). Each of the lettered panels on the right gives an example of the dynamics represented by the shading of the region plot on the left. Within the gray region at the bottom left of the plot (P), all species except the generalist pollinator are extinct (a). Within the light gray area (SP), all species stably persist with either no oscillations (b; left of the vertical dotted line) or damped oscillations (c, e; right of the horizontal dotted line). Within the white region (PO), species exhibit persistent oscillations (d). Within the dark gray region (PD), the shared plant is extinct and the system collapses to a predator-prey system (f) $\{e_M = 0.5, e_{MP} = 1, e_{SD} = 1, e_{PM} = 0.2, e_{DS} = 0.2, e_{DP} = 0.2, e_{PD} = -1, d_s = 1, d_P = 1, d_D = 1, d_M = 1, q_P = 0.1, q_D = 0.1, \alpha_P = 2, \alpha_D = 0, \alpha_{MP} = 4\}$.

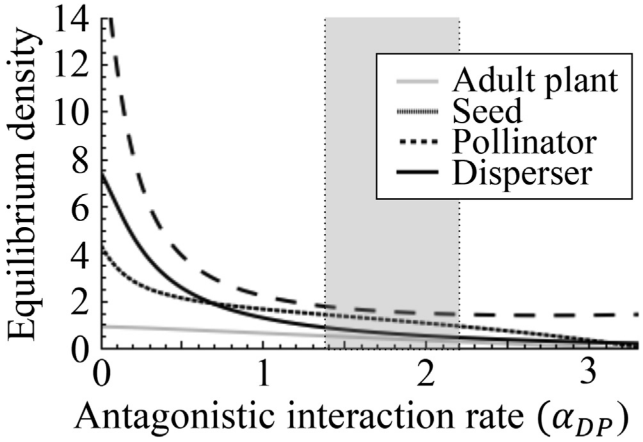

Fig. 3. The equilibrium density of pollinators, dispersers, adult plants, and seeds as functions of the rate of the antagonistic interaction (α_{DP}). The gray region indicates where the system shows persistant oscillations $\{e_M = 0.5, e_{MP} = 1, e_{SD} = 1, e_{PM} = 0.2, e_{DS} = 0.2, e_{DP} = 0.2, e_{PD} = -1, d_s = 1, d_P = 1, d_D = 1, d_M = 1, q_P = 0.1, q_D = 0.1, \alpha_P = 2, \alpha_D = 0, \alpha_{MP} = 4, \alpha_{SD} = 2\}$.

2.2. Analysis of direct and indirect effects

Analysis of the Jacobian, or "community", matrix provides a method for determining direct, indirect and net effects of any of the modeled species on another (Yodzis, 1988). To do so, this analysis determines what the response of one populations' equilibrium densities would be to a press (i.e., sustained) perturbation in the equilibrium density of another species and can be conducted in both directions for all species pairs (See Supplementary Material S3). Direct effects are determined by the Jacobian matrix, and net effects are determined by the negative of the inverse of the Jacobian matrix, both evaluated at the equilibrium densities. The indi-

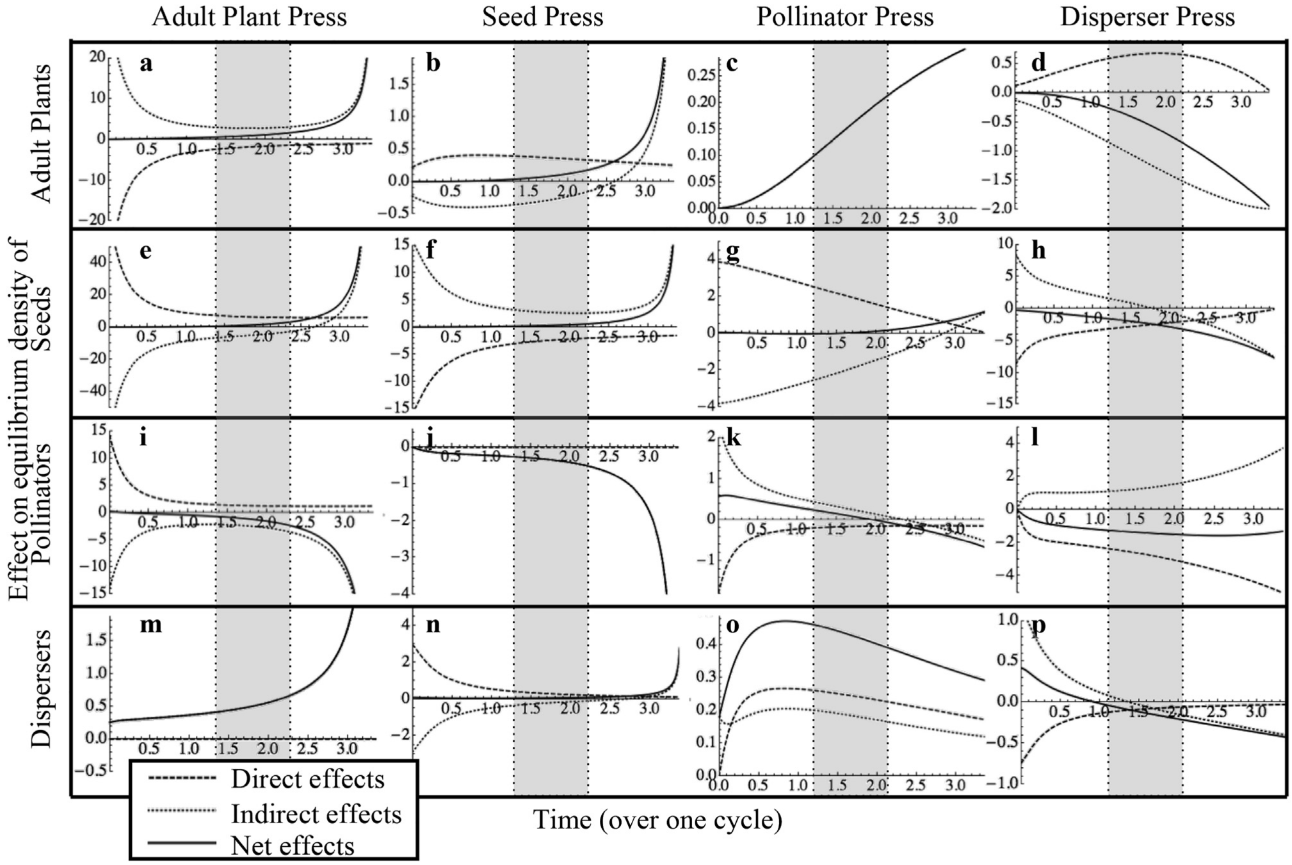

Fig. 4. The net, direct, and indirect effects of all possible press perturbations on each population depending on the rate of the antagonistic interaction (α_{DP}). Each column refers to the species being perturbed and each row refers to the species being affected. The gray regions represent the region of parameter space over which the system shows persistent oscillations in all species $\{e_M = 0.5,\ e_{MP} = 1,\ e_{SD} = 1,\ e_{PM} = 0.2,\ e_{DS} = 0.2,\ e_{DP} = 0.2,\ e_{PD} = -1,\ d_S = 1,\ d_P = 1,\ d_D = 1,\ d_M = 1,\ q_P = 0.1,\ q_D = 0.1,\ \alpha_P = 2, \alpha_D = 0, \alpha_{MP} = 4, \alpha_{SD} = 2\}$.

rect effects are therefore the difference between the net and direct effects. Positive values indicate that the effect on the population of interest occurs in the same direction as the perturbation. Over the parameter values for which persistent oscillations exist, the interpretation of a press perturbation on one species' density is not straightforward. Therefore, we conduct the same analysis of direct, indirect, and net effects on the unstable equilibria values in the interior of the cycles, as well as over the range of densities occurring within a cycle. We focus our analysis of direct and indirect effects on the case of generalist pollinators and specialist dispersers for three reasons. It is the only case in which all species can persist under moderate levels of antagonism, it exhibits the most complex population dynamical consequences, and it best captures the mistletoe system (see *Results: Direct and indirect effects of antagonism*).

3. Results

3.1. Stability analysis: no direct interaction between disperser and pollinator

When dispersers and pollinators do not interact directly in the model, the three-species system of interactions (hereafter, the mutualistic system) can persist under a broad range of conditions, provided that the mutualistic interaction rates (α_{SD} and α_{MP}) are sufficiently high (Figs. A1–A4). There are two key results here. First, the mutualistic system is better able to persist at low rates of seed dispersal (α_{SD}) than at low rates of pollination (α_{MP}). Second, the mutualistic system persists under a wider range of pollination and dispersal rates when pollinators are generalists ($\alpha_P > 0$) rather than specialists (Figs. A3-A4 vs A1-A2). Whenever pollinators are specialists, regardless of specialization in dispersers, they can persist only under relatively high rates of pollination, but not necessarily dispersal. The reasons for these results are two-fold. First, greater pollinator density, either from higher pollination rates or a generalist diet, leads to a seed density sufficient for disperser persistence. Second, the establishment of adults is ultimately limited by space, so increasing disperser density, either through higher dispersal rates or a generalist diet, provides limited benefits to plant density.

3.2. Consumption of pollinators by dispersers

When pollinators are consumed by seed dispersers, the system can exhibit several qualitatively different population dynamical behaviors depending on (1) the rate of predation relative to that of the mutualistic interactions and (2) the relative dependence of the pollinators and dispersers on the mutualistic interaction versus outside resources. When both pollinators and dispersers are specialists ($\alpha_P = 0, \alpha_D = 0$), no species can persist under any of the parameter combinations that we considered (Fig. 1a). In this case, external resources are unavailable to buoy pollinator and disperser densities sufficiently to sustain the plant unless pollination rates are greater than those we investigated in depth (e.g. persistence occurs when $\alpha_{MP} = 10$, $\alpha_{DP} = 0.5$, $\alpha_{SD} = 1$). When dispersers are generalized ($\alpha_D > 0$), the mutualistic system is only able to persist under very low predation rates (α_{DP}; Fig. 1b, c, e, f, g, i). At high rates of predation, the community collapses, such that only the dis-

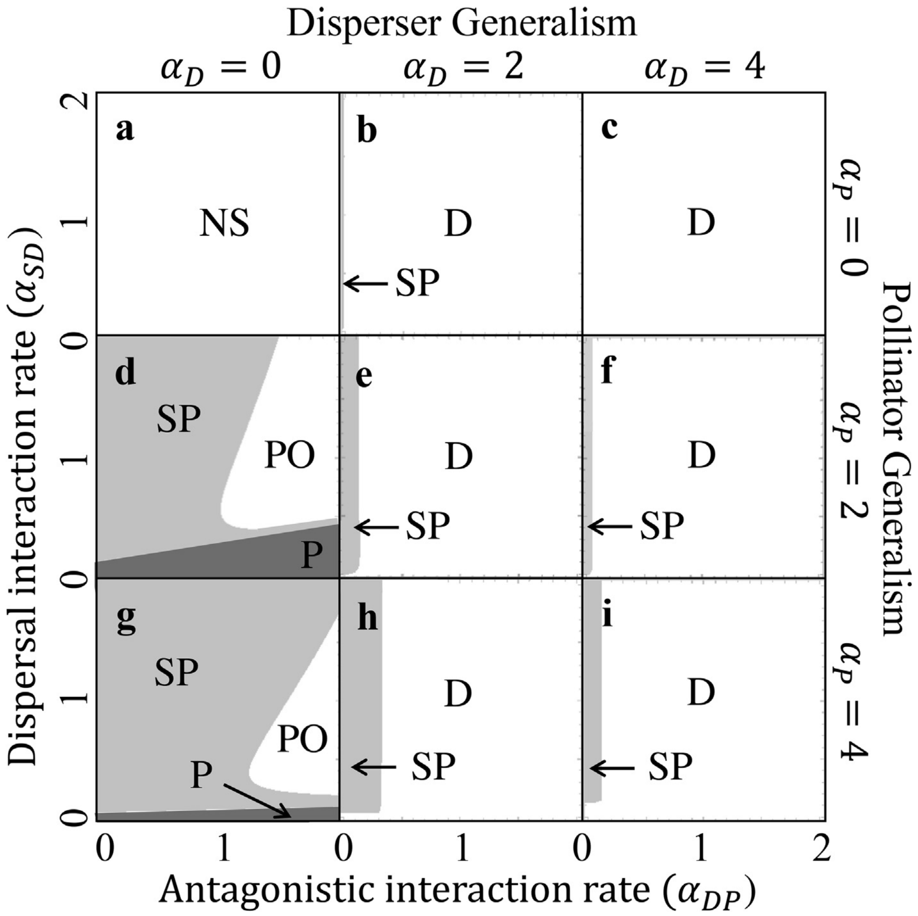

Fig. 5. Region plots depicting the population dynamical consequences of non-consumptive negative effects of dispersers on pollinators as a function of dispersal (α_{SD}) and antagonistic interaction rates (α_{DP}). The columns represent levels of diet specialization in the disperser with $\alpha_D = 0$ indicating full specialization on the modeled species and increasing values of $\alpha_D$indicating increasing generalism or use of resources external to the model. The rows similarly represent levels of diet specialization in the pollinator. Dynamical outcomes are labeled as follows: NS indicates that no species persists, P is a pollinator-only community, D is a disperser-only community, SP represents stable persistence of all species, and PO represents persistent oscillations in all species $\{e_M = 0.5,\ e_{MP} = 1,\ e_{SD} = 1,\ e_{PM} = 0.2,\ e_{DS} = 0.2,\ e_{PD} = -1,\ d_S = 1,\ d_P = 1,\ d_D = 1,\ d_M = 1,\ q_P = 0.1,\ q_D = 0.1, \alpha_{MP} = 4\}$.

perser persists on its external resource. The more generalized the pollinator in these cases (greater α_P), the greater the rates of predation at which the mutualism can persist (Fig. 1e vs h; Fig. 1f vs i), because pollinator population densities are sustained by external resources. The mutualistic system can persist under moderate to high rates of predation only when dispersers are specialized and pollinators have external resources ($\alpha_P > 0, \alpha_D = 0$; Fig. 1d, g). In these cases, when the dispersal rate is low relative to the predation rate, the system collapses to a predator–prey system in which the prey (pollinators) exploit external resources and predators (dispersers) are specialized on pollinators. At very low rates of both dispersal and predation, only generalist pollinators can persist, but all three species can persist when the dispersal rate is high relative to the predation rate. The key point here is that the mutualistic system is only able to persist at moderate levels of antagonism when pollinators are generalists and dispersers are specialists.

3.3. Case study of consumption of generalist pollinators by specialist dispersers

The most complex population dynamical results occur when generalist pollinators ($\alpha_P > 0$) are consumed by specialist dispersers ($\alpha_D = 0$) (Fig. 1). At very low rates of both dispersal and predation, the shared plant and the seed disperser cannot be sustained, so only the pollinator persists (Fig. 2a). When dispersal rate is intermediate and predation rate increases from low to high, several distinct types of population dynamics are observed. When predation rate is very low, stable persistence is possible provided that species' densities exceed an Allee threshold below which only the pollinator can persist on its external resource (Fig. 2b; Fig. A5a). As predation rate increases, the three species persist, showing damped oscillations (Fig. 2c; Fig. A5b) and eventually persistent oscillations (Fig. 2d; Fig. A5c). Oscillations occur because predation reduces not only pollinator density but also seed density in turn. Eventually this deprives dispersers of both fruit and prey resources such that their population declines. The decline in dispersers then reduces predation, allowing pollinators and, therefore, seeds to increase in density. Cyclic dynamics are not possible when any one of the three interactions ($\alpha_{DP}, \alpha_{MP}, \alpha_{SD}$) are absent; therefore, only the combination of mutualism and antagonism allows for persistent oscillatory behavior. As predation rate is increased further, the dynamics return to damped oscillations (Fig. 2e; Fig. A5d). This transition occurs because antagonism buoys disperser density sufficiently that self-limitation (q_d) constrains the amplitude of the cycling. At high levels of antagonism, the plant is driven to local extinction when seed densities decline due to declining pollinator density. At this point, the system behaves as a classic predator-prey system with self-limitation and a Type I functional response, exhibiting damped oscillations (Fig. 2f; Fig. A5e). For a given level of dispersal, the equilibrium density of all species decreases with increasing predation until only the predator-prey system remains (Fig. 3).

The dynamics described above occur at a moderate pollination interaction rate ($\alpha_{MP} = 4$) (Fig. A6b). When the pollination rate is decreased ($\alpha_{MP} = 2$), the mutualistic system is able to persist only at very low predation rates, and persistent oscillations do not occur in the regions of parameter space we explore (Fig. A6a). At high pollination rates ($\alpha_{MP} = 8$), the mutualistic system can persist under higher rates of predation. Yet, this increase in feasible parameter space is primarily driven by expansion of the region in which persistent oscillations occur (Fig. A6c).

3.4. Direct and indirect effects of antagonism

Press perturbation analyses show that the antagonism propagates through the network, influencing the magnitude and sometimes the direction of indirect interaction effects. There are three key regimes. First, at low levels of antagonism, press perturbations often illuminate the presence of direct and indirect effects of similar, typically large, magnitude in opposing directions (Fig. 4a-b, d-i, k-l, n, p). As the density of all species is greatest when antagonism is infrequent, these opposing effects are largely the result of self-limitation pressures on the species' densities preventing them from benefiting from positive perturbations to plant density. Where opposing direct and indirect effects occur, mean net effects remain small to moderate over the region of persistent oscillations in population densities (Fig. 4). The second regime involves limit cycles. Over the course of a single limit cycle, the net effects of press perturbations on species are similar to the mean value over most of the cycle (Fig. A7). However, large fluctuations driven entirely by indirect effects occur in the net effects at the point of the cycle immediately preceding the peak in pollinator density (Fig. A7). Pollinator populations peak first in the cycle, followed by populations of seeds produced as a result of pollination, then of dispersers that consume seeds, and finally of adult plants established after dispersal. The large fluctuations in the effects of changing densities drive the cycles. Third, at the highest predation rates, net effects seen during press perturbations in many cases become large and driven primarily by indirect effects (Fig. 4a-b, d-f, i, n). At these high predation rates, the plants have fallen to such low density that positive press perturbations to their density show large net effects in the whole system. In only one case do the direct and indirect effects never oppose each other in direction: positive press perturbations of pollinator density always show a positive direct effect on dispersers through consumption and a positive indirect effect on dispersers through seed production (Fig. 4o).

Net effects are entirely driven by indirect effects for three pairs of populations: pollinators have no direct effect on adult plant density, as they only increase seed density (Fig. 4c); seeds have no direct effect on pollinator density (Fig. 4j); and adult plants, rather than the seeds they produce, have no direct effect on dispersers (Fig. 4m). In each of these cases, the magnitude of the indirect and, therefore, also the net effects increase as the rate of predation increases. Pollinator and adult plant populations indirectly have increasingly positive effects on the density of adult plants and disperser populations, respectively, as predation rate increases. However, by fueling disperser populations, seeds have an increasingly negative indirect effect on pollinators with increasing predation rate (Fig. 4m).

3.5. Non-consumptive negative effect on pollinators

Similar to the results when dispersers consume pollinators, the shared plant species can persist only under low rates of non-consumptive antagonism when dispersers have a generalist diet (Fig. 5b, c, e, f, h, i). Even when the negative effect on pollinators does not boost disperser density, it decreases pollinator density below that necessary for plant reproduction. In these cases when the shared plant and pollinator cannot persist, only the generalist disperser remains. With a generalist disperser, the shared plant can persist under marginally greater non-consumptive interaction rates when the pollinator is more generalized (Fig. 5e vs h; Fig. 5f vs i). Whereas none of the species can persist when both pollinators and dispersers are specialized and pollinators are negatively affected by dispersers (Fig. 5a), systems with generalist pollinators and specialist dispersers are most tolerant of non-consumptive effects, just as they are of consumptive ones (Fig. 5d, g). In these cases, the mutualism stably persists except at high rates of negative effects on pollinators, where persistent oscillatory dynamics occur when species' densities exceed an Allee threshold below which only the pollinator persists.

4. Discussion

Although the majority of theoretical and empirical work on mutualisms to date has focused on pairwise interactions, individuals of a given species often interact with multiple functionally distinct mutualists at different stages of their lives. When these species can interact directly with one another externally to the mutualism, those interactions will feed back to indirectly affect the shared species. These interactions are potentially critical for determining the dynamics of the entire mutualistic system. Using a simple population dynamical model, we have investigated how antagonism between two species that interact mutualistically with a shared species impact the population dynamics, stability, and magnitude of direct and indirect interactions in the three-species system. Notably, while we chose a simple, restrictive model, our initial analyses of systems with facultative mutualisms and non-substitutable resources (Supplementary Material S1) indicate that our results may be more broadly applicable to other networks of coupled mutualism and antagonism. In general, we find that 1) the relative rates of the mutualisms and antagonisms interact to determine the magnitude of indirect effects and therefore the qualitative dynamics of the system, and 2) persistence of the system depends upon the degree of specialization of the two functionally different mutualists. Our work highlights how indirect effects lead to dynamical outcomes of multispecies interactions that could not be expected from a pairwise perspective.

4.1. The effect of indirect interactions on population dynamical outcomes

As predicted, large negative indirect effects caused by the antagonism between species sharing a mutualist lead to the extinction of the shared species and the mutualistic interactions. Persistent oscillations driven primarily by indirect effects can occur when both mutualism and antagonism are of moderate rate, despite the fact that limit cycles are impossible when either the antagonism or mutualism operate alone in our model. Our work provides a novel mechanism by which oscillatory dynamics can occur in models of mutualism, adding to previously described mechanism such as the structure of life cycles captured by discrete time (e.g., Gilpin et al., 1982) or time lags (e.g., Li, 2001) and the inclusion of competition (e.g., Bachelot et al., 2015; Mitani and Mougi, 2017). In our study, when the antagonism is weak relative to the mutualistic interactions, direct effects outweigh indirect effects and all large direct interactions are positive. Negative indirect effects due to self-limitation typically negate these positive effects when the species are at high densities, leading to negligible net effects. At high levels of antagonism, indirect effects tend to dominate. The increased antagonism causes decreased equilibrium densities of all members of the community, so self-limitation no longer dominates the indirect effects and, eventually, extinction of the shared species and the mutualistic interactions occurs. Together, these results indicate that large direct and indirect effects may counterintuitively yield negligible changes in overall species' densities. Empirical studies focusing only on direct or net effects of changes in species densities will fail to predict population dynamics.

4.2. The role of specialization

This model can help us to understand how negative interactions between pollinators and dispersers could impact the plants that they share and to make predictions about the types of interaction architecture that should be most common in nature. Of the four potential combinations of specialization and generalism in pollinators and dispersers, we find that only one is likely to persist given the types of antagonism we investigate: generalized pollinators and specialized dispersers. In nature, this interaction architecture is rare, even in the absence of any antagonism between the mutualists; generalism of both pollinators and dispersers is most common and pollination is more specialized on average than dispersal (Wheelwright and Orians, 1982; Jordano, 1987). Traits needed to access the floral resources of a given plant are often more specialized than those needed to consume fruit, and greater morphological divergence has arisen among biotically pollinated flowers than among fruit of biotically dispersed plants (Whitney, 2009). The fact that the only interaction network able to tolerate the antagonism in our model is considered rare for these other reasons is in agreement with the presumed scarcity in nature of the antagonisms we explore. Despite our prediction that systems with generalized pollinators will persist under higher rates of antagonism, we found that systems with generalized dispersers were similarly unstable in the face of moderate levels of antagonism regardless of the degree of pollinator specialization. Any level of generalism in the antagonist species (i.e., the disperser) allows it to gain sufficient density that the negative indirect effect on the shared mutualist are large enough to cause extinction at low to moderate frequencies of antagonism. To the best of our knowledge, there is no plant species that obligately relies upon both specialized pollinators and specialized dispersers. The infrequency of doubly specialized systems may be due to a high risk of reproductive failure (Bond, 1994; Astegiano et al., 2015) or limitations that specialization puts on the shared mutualist's niche breadth (Batstone et al., 2018). Our results suggest that these specialized communities will be further disadvantaged, as no species could persist under any level of antagonism between specialist mutualists, and they require the highest rates of mutualistic interactions to persist even in the absence of such antagonism.

4.3. Empirical examples of antagonism between species sharing a mutualist species

The little available work investigating whether pollinating insects are consumed by seed dispersers suggests that this phenomenon may be rare (e.g., see Boyle et al., 2011 appendix). However, our model shows that the ecological characteristics of the desert mistletoe-phainopepla-insect system in the southwestern US and northwestern Mexico (Yule and Bronstein, 2018a,b) may be particularly resilient to this type of interaction, as it matches the restrictive conditions necessary for persistence. Due to the generalist diet of its pollinators and specialist diet of its dispersers, desert mistletoe could persist under moderately frequent consumption or non-consumptive negative effects on the behavior of these pollinators by dispersers.

In contrast to desert mistletoe, figs rely on highly specialized pollinators (Bronstein, 1987) and a diverse array of generalist dispersers (Shanahan et al., 2001). Many fig wasps, including some pollinators, are still present in the figs at the point when they ripen and are consumed (Bronstein, 1988). However, the results of our model show that such consumption must not be frequent if the mutualistic system is to persist. This result is consistent with the occurrence of strategies by figs to increase consumption by seed dispersers of fruit without wasps relative to fruit containing wasps (Dumont et al., 2004).

We emphasize, though, that pollinator-disperser antagonism is just one type of antagonism that exists between mutualists in nature; this model can easily be extended to explore their dynamics. The best-documented examples involve ant protectors and pollinators that share a plant. In these systems, plants provide benefits to ants in form of nutritional rewards (e.g., extrafloral nectar, food bodies) and/or shelter (e.g., domatia, hollow thorns) in exchange for protection from herbivorous insects (Rico-Gray and Oliveira, 2007). Aggressive ant protectors often provide the best herbivore defense; however, this comes at the potential cost of deterring, attacking, and sometimes consuming pollinators (Ness, 2006; Malé et al., 2012; LeVan et al., 2014). Furthermore, ant-protectors of plants can exploit floral nectar and pollen or castrate flowers, leading to reduced attraction of and rewards for pollinators (Gaume et al., 2005; Malé et al., 2012), similar to the non-consumptive negative effects we explore. In obligate ant-plant mutualisms, pollinators tend to be generalists and ants are specialized (Bluthgen et al., 2007; M.E. Frederickson, pers. comm.). Similarly, a model designed to predict the degree to which ants should evolve to avoid pollinators showed that pollinators are most likely to persist when attacked if ants depend obligately on the plant (Oña and Lachmann, 2011). When ants are not specialized, our results show that the protection mutualism and the pollination mutualism should only be able to persist if the ants' impact on pollinators is very low.

4.4. Non-consumptive interactions

Non-consumptive effects result in dynamical outcomes that are qualitatively similar to those seen with predation under most conditions. Contrary to our predictions, non-consumptive interactions do not cause persistence to be more likely than it is under predation and, in fact, can cause more complex dynamics when antagonistic interaction rates are moderate. Therefore, we find that even subtle non-consumptive negative effects, which can be difficult to observe in empirical studies, can lead to extinction in a mutualistic system. It should be noted that in our model, non-consumptive negative effects of dispersers on pollinators are direct, in that increasing disperser density can be thought of as decreasing pollinator per-capita birth rate independent of pollination interaction with the plants. Alternatively, increased disperser or ant density could have no direct effect on pollinator density and instead reduce the rate of interaction between the pollinators and plants (Jones and Dornhaus, 2011). This type of interference would likely cause different dynamical outcomes than the situation that we model and is worthy of future exploration.

5. Conclusion

Predicting the outcomes of multispecies interactions is a major challenge in community ecology. The net effects of pairwise mutualistic interactions are known to be highly dependent upon ecological context (Chamberlain et al., 2014; Hoeksema and Bruna, 2015). We show that tripartite interactions should be no less labile. Indeed, theory that includes "interactions among interactions" will allow us to predict otherwise unforeseen consequences of changes to species interactions networks, such as extinction or oscillatory population dynamics in mutualisms that would otherwise persist stably. This and future theoretical work using mechanistic models for systems of coupled mutualism and antagonism will facilitate the generation of broad hypotheses about when indirect effects should drive outcomes of such multispecies interactions. Despite the ubiquity of interaction networks that contain multiple mutualisms, we lack the empirical studies to evaluate many of the predictions outlined by these models (García-Callejas et al., 2018). In the future, such studies will allow for a better understanding of the population and evolutionary dynamics of mutualisms and provide insights that have proven elusive under the traditional pairwise interaction framework.

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Appendix A. Supplementary data

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