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# Population Dynamics of Plant and Pollinator Communities: Stability Reconsidered

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**ABSTRACT:** Plant-pollinator networks are systems of outstanding ecological and economic importance. A particularly intriguing aspect of these systems is their high diversity. However, earlier studies have concluded that the specific mechanisms of plant-pollinator interactions are destabilizing and should lead to a loss of diversity. Here we present a mechanistic model of plant and pollinator population dynamics with the ability to represent a broad spectrum of interaction structures. Using this model, we examined the influence of pollinators on the stability of a plant community and the relationship between pollinator specialization and stability. In accordance with earlier work, our results show that plant-pollinator interactions may severely destabilize plant coexistence, regardless of the degree of pollinator specialization. However, if plant niche differentiation, a classical stabilizing mechanism, is sufficiently strong to overcome the minority disadvantage with respect to pollination, interactions with pollinators may even increase the stability of a plant community. In addition to plant niche differentiation, the relationship between specialization and stability depends on a number of parameters that affect pollinator growth rates. Our results highlight the complex effects of this particular type of mutualism on community stability and call for further investigations of the mechanisms of diversity maintenance in plant-pollinator systems.

**Keywords:** community, mutualism, pollination, specialization, stability.

## Introduction

A central problem in ecology is understanding the impact of interspecific interactions on the dynamics of the populations and communities involved. Despite an early interest in mutually beneficial relationships between species (e.g., Pound 1893), mutualism has only recently begun to receive the same amount of attention as, for example, predator-prey or competitive interactions. Considering the ubiquity of mutualistic interactions in natural ecosystems (Bronstein et al. 2006), the question of their effect on community stability is one of great importance. It has far-

reaching implications both for the development of ecological theory and for applied problems of biodiversity conservation.

One of the most common types of mutualistic interactions in terrestrial ecosystems is that between plants and their animal pollinators (Ollerton et al. 2011). Plant-pollinator systems often comprise complex networks of interactions between highly diverse species assemblages (Bascompte and Jordano 2007), yet it is still an open question how diversity in these systems is generated and maintained. On the basis of simple models of competition between two plant species for a generalist pollinator, several previous studies have predicted that plant coexistence should be destabilized by interactions with pollinators (Levin and Anderson 1970; Waser 1978; Goulson 1994; Kunin and Iwasa 1996). In these model systems, the fact that the same animal must visit two conspecific flowers in close succession for pollination to occur results in lower pollination success of an initially rarer plant species and the subsequent decline of that plant. This specific property of pollination was not considered in recent articles about the stability of mutualistic communities that used more general models of mutualism (Bascompte et al. 2006; Okuyama and Holland 2008; Bastolla et al. 2009). Thus, it remains unclear what factors maintain diversity in natural plant-pollinator systems despite the inherent reproductive disadvantage of less abundant plant species.

One factor that could possibly reduce competition between coflowering plant species is specialization of plant-pollinator interactions (Rathcke 1988). Natural plant-pollinator systems exhibit a continuum from exclusive one-to-one relationships to diffuse mutualisms involving hundreds of species (Waser et al. 1996; Johnson and Steiner 2000), with the majority of networks at an intermediate level of specialization (Blüthgen et al. 2007). By specializing on a subset of all available pollinators, the loss of pollen to heterospecific flowers can be reduced (Muchhala et al. 2010).

In this article, we develop a flexible model of plant and pollinator population dynamics that allows the inclusion

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of any number of species in the two communities and representation of many kinds of interaction network structures. Our model is based on a mechanistic representation of plant-pollinator interactions that accounts for the specific properties of this type of mutualism. Using this model, we investigate two main questions: (1) What effect does the addition of interactions with pollinators have on the stability of a plant community? And (2) how does the degree of specialization of plant-pollinator interactions influence stability of plant-pollinator systems? In analogy to the abovementioned studies, we began with a simple model community of two competing plant species and compared the stability of coexistence of these two plants alone with the stability of a system with pollinators of varying degrees of specialization. In order to establish stable coexistence of plant species in the first place, we introduced a classical stabilizing mechanism, niche differentiation of the two plant species with respect to abiotic resources (Chesson 2000), and determined the stability of plant-pollinator systems at different levels of plant niche differentiation. Furthermore, we examined the influence of other model parameters, such as the degree of pollen carryover and the amount of nectar per plant, on community stability. These analyses shed light on the complex ways in which mutualistic interactions can affect species coexistence. In the future, our model may serve as a basis for investigating the stability of empirical plant-pollinator networks and the influence of interaction structure on the robustness of these systems.

### The Model

We first derive equations describing the dynamics of a plant community without pollinators, comprising  $m$  species. All adult plants reproduce at equal per capita rates  $b_{\text{veg}}$  through self-pollination or vegetative propagules and die at a constant rate  $d_p$ . The offspring compete for suitable sites for establishment. New plants can establish only if the total density of all plant species lies below the habitat capacity  $H_p$ . The overlap in habitat requirements of two plant species  $i$  and  $k$  is described by parameter  $\gamma_{ik}$ , the competition coefficient of the classical Lotka-Volterra model that varies from 0 (complete niche separation) to 1 (complete niche overlap). The growth of a plant population of species  $i$  within one time step,  $\Delta P_i$ , is thus represented by a difference equation of the form

$$\Delta P_i = b_{\text{veg}} \left( 1 - \frac{\sum_{k=1}^m \gamma_{ik} P_k}{H_p} \right) P_i - d_p P_i. \quad (1)$$

When pollinators are present, a second term is added to the birth rate of plant populations. This term represents the per capita amount of pollen received by a plant, which

is in turn determined by pollinator abundance and behavior.

A key assumption of our model is that the likelihood of an interaction between a specific plant-pollinator species pair depends on both the species' relative abundances in their respective communities (a variable component) and the species-specific traits of the plant and pollinator (a fixed component). In the model, this concept is implemented in the following way (fig. 1): from the pool of plant individuals, a plant is randomly selected for each pollinator individual. Thus, the probability that a pollinator encounters a plant of species  $i$  is equal to species  $i$ 's relative abundance,  $P_i / (\sum_{k=1}^m P_k)$ . The pollinator's decision to visit the selected plant depends on the degree of trait matching between the plant and the pollinator species (Vazquez et al. 2009). It comprises both traits that influence the attraction to the plant, for example, preferences for certain flower colors or scents (Junker et al. 2010), and traits that may act as barriers to a pollinator visit, such as a complex flower morphology (Stang et al. 2007). In the model, the degree of trait matching is represented by parameter  $\alpha_{ij}$ , which takes a specific value between 0 and 1 for each plant-pollinator species pair. The total probability that an animal of species  $j$  finds and accepts a plant of species  $i$  is thus  $(P_i / \sum_{k=1}^m P_k) \alpha_{ij}$ . If a pollinator does not visit the plant it encounters, it cannot visit another plant during the same time step. By constructing different matrices of  $\alpha_{ij}$  values, it is possible to implement any kind of interaction network structure in the model and to explore the consequences of varying degrees of pollinator specialization for community stability.

A distinctive attribute of pollination is that a plant can be fertilized only if the pollinator has visited a plant of the same species before the current flower visit. Moreover, pollen may be lost in intervening visits to flowers of other species (Campbell and Motten 1985; Feinsinger et al. 1988; Karron et al. 2009). Therefore, in our model, a flower visit results in pollination only if the visiting animal has been on a plant of the same species during at least one of its last  $B$  visits, not counting time steps without a successful flower visit. Variation of parameter  $B$  allows for an investigation of the effects of different degrees of pollen carryover on the stability of plant-pollinator systems. The probability that a pollinator of species  $l$  has visited a flower of species  $i$  in at least one of its last  $B$  visits is  $1 - [1 - (P_i \alpha_{il} / \sum_{k=1}^m P_k \alpha_{kl})]^B$ . The expected amount of pollen received by a plant of species  $i$  within one time unit, summed over all  $n$  pollinator species with densities  $A_p$  is thus

$$F_i = \frac{1}{P_i} \sum_{l=1}^n \left\{ \frac{P_i}{\sum_{k=1}^m P_k} \alpha_{il} \left[ 1 - \left( 1 - \frac{P_i \alpha_{il}}{\sum_{k=1}^m P_k \alpha_{kl}} \right)^B \right] A_l \right\}. \quad (2)$$

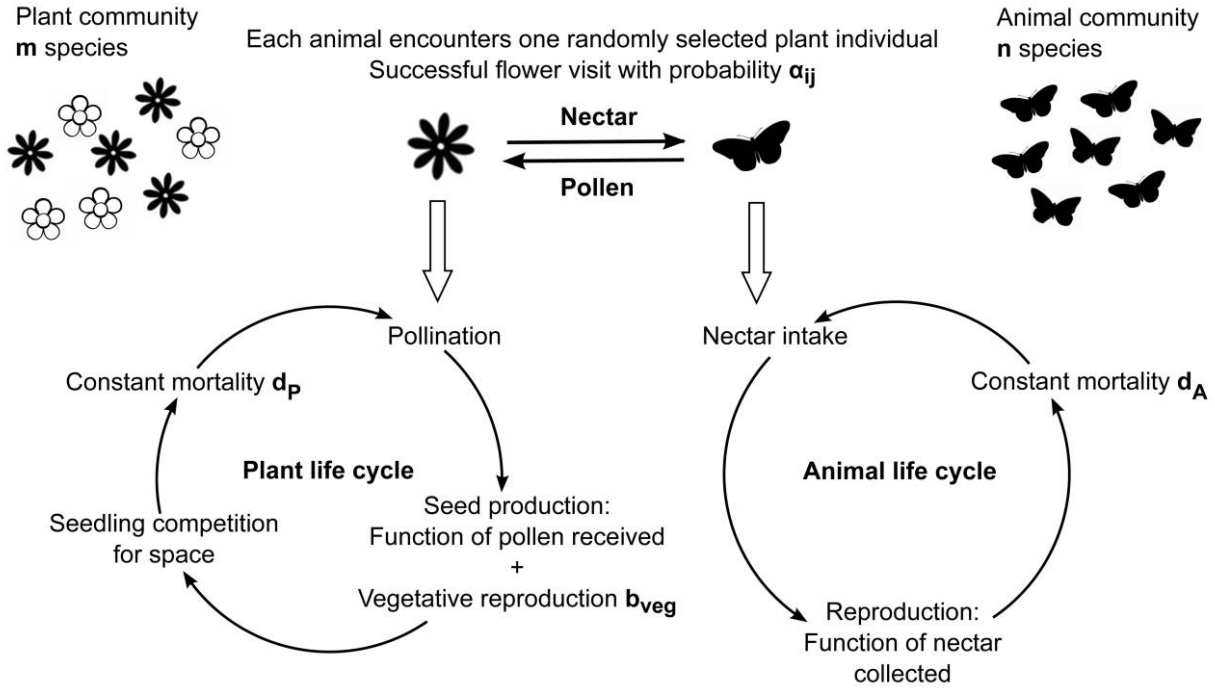


Figure 1: Schematic overview of the model of plant and pollinator population dynamics.

The growth of a plant population in the presence of pollinators is then described by

$$\Delta P_i = (F_i \beta_p + b_{veg}) \left( 1 - \frac{\sum_{k=1}^m \gamma_{ik} P_k}{H_p} \right) P_i - d_p P_i, \quad (3)$$

where  $\beta_p$  denotes the conversion of pollen to seeds. Throughout the main body of this article, we assume a linear (Holling type I) functional response for both plant and animal reproduction (see below). As demonstrated in appendix A, a saturating (Holling type II) functional response does not fundamentally change the results of our analyses.

During a flower visit, an animal receives a nutritional reward, subsequently termed “nectar,” although this reward could in reality include both nectar and pollen. Here the assumption is that collection of the reward does not have a negative effect on the plant’s reproductive success, as might be the case for pollen collection. For simplicity, the amount of nectar per plant is assumed to be constant; that is, nectar is refilled instantly at the end of each time step. If several pollinators visit the same plant within a single time step, the total nectar volume  $N$  is divided equally among all visitors. Assuming that the distribution of pollinators on plants follows a Poisson distribution with mean  $\mu_i$  for plants of species  $i$ , the expected amount of

nectar received by a focal pollinator on a plant of species  $i$  is calculated as

$$E(\mu_i) = \sum_{k=0}^{\infty} \frac{N}{k+1} \frac{\mu_i^k e^{-\mu_i}}{k!}, \quad (4)$$

where  $k$  denotes the number of additional pollinator individuals visiting the same flower. This expression simplifies to

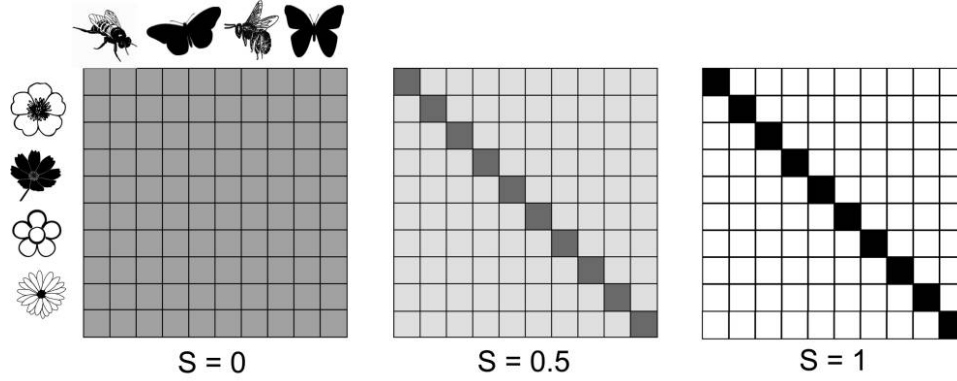
$$E(\mu_i) = \frac{N}{\mu_i} (1 - e^{-\mu_i}). \quad (5)$$

Setting

$$\mu_i = \frac{\sum_{k=1}^n A_k \alpha_{ik} (P_i / \sum_{h=1}^m P_h)}{P_i}, \quad (6)$$

$$\mu_i = \frac{\sum_{k=1}^n A_k \alpha_{ik}}{\sum_{h=1}^m P_h}, \quad (7)$$

and summing up over all plant species weighted by the probability of a visit to each plant gives the expected amount of nectar collected by a pollinator of species  $j$  within one time unit:



**Figure 2:** Illustration of the method used to vary the degree of specialization ( $0 \leq S \leq 1$ ) of plant-pollinator networks in numerical simulations. Each grid cell symbolizes an interaction between plant (rows) and pollinator species (columns). The shade of gray indicates the degree of trait matching  $\alpha_{ij}$  of the plant and pollinator species that varies between 0 (white) and 1 (black).  $\alpha_{ij}$  summarizes all species-specific traits that determine the likelihood of a successful flower visit, such as the proboscis length of a pollinator in comparison to the corolla length of the plant. Note that these are matrices of trait-matching values, and not realized interactions: the distribution of realized interactions depends on species abundances as well as on trait matching.

$$R_j = \sum_{i=1}^m \frac{P_i}{\sum_{h=1}^m P_h} \alpha_{ij} \frac{N}{(\sum_{k=1}^n A_k \alpha_{ik}) / (\sum_{h=1}^m P_h)} \left[ 1 - \exp\left(-\frac{\sum_{k=1}^n A_k \alpha_{ik}}{\sum_{h=1}^m P_h}\right) \right]. \quad (8)$$

In analogy to the dynamics of plant populations, animal reproduction is a function of the per capita amount of nectar, with  $\beta_A$  denoting the conversion of nectar to offspring. All animal populations experience a constant mortality rate  $d_A$ . Thus, the dynamics of the  $j$ th pollinator population is described by

$$\Delta A_j = R_j \beta_A A_j - d_A A_j. \quad (9)$$

Note that unlike plant birth rates, pollinator growth rates are assumed to be density independent. However, density regulation of the overall pollinator population results from the limited amount of nectar provided by all plants, which in turn is limited by the habitat capacity. Thus, density regulation of plant populations is sufficient to ensure that pollinator populations also do not grow unbounded.

### Model Analyses

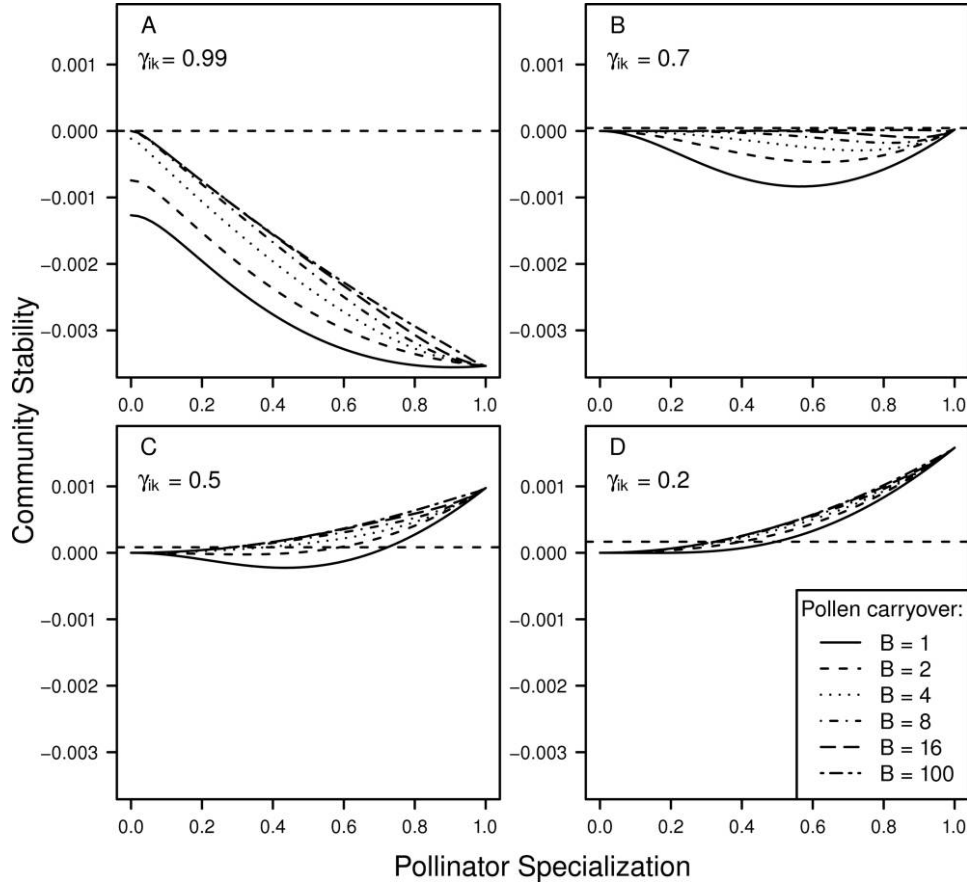
We performed numerical analyses in order to examine how the stability of plant communities is affected by the addition of interactions with pollinators of varying degrees of specialization. Parameter values were chosen so as to represent realistic values for a time step length of 10 seconds, the time span assumed for a pollinator to find and visit a single flower. Population densities at equilibrium were found by iterating the system of difference equations until the difference between population densities in two

successive iterations fell below a threshold value of  $10^{-5}$ . Through systematic variation of initial population densities, we determined the starting conditions leading to an equilibrium state that allowed all plant and animal species to persist. The analyses presented in this article are for systems of two plant and two animal species, but the results do not change qualitatively if further species are added.

Community stability was measured by calculating the dominant eigenvalue  $\hat{\lambda}$  of the Jacobian matrix at the equilibrium point with coexistence of all species (May 1972, 1974; Otto and Day 2007; Okuyama and Holland 2008). The dominant eigenvalue  $\hat{\lambda}$  determines the type of equilibrium (stable or unstable) as well as the rate of movement of the system back to the equilibrium (if the equilibrium is stable) or departure from the equilibrium (in case of an unstable equilibrium) following a small perturbation. For a discrete time model,  $|\hat{\lambda}| < 1$  indicates a stable equilibrium and  $|\hat{\lambda}| > 1$  indicates an unstable equilibrium.

Numerical analyses were performed over a wide range of parameter values and initial conditions. We used Maxima 5.20.1 (Maxima.sourceforge.net 2010) for symbolic calculations and R 2.11.1 (R Development Core Team 2010) for numerical analyses and preparation of figures.

To be able to vary the degree of specialization of plant-pollinator networks continuously from a fully connected network with identical trait-matching values for all interactions to a maximally specialized network with exclusive one-to-one relationships, we defined a measure of specialization  $S$  in the following manner (fig. 2): in a plant-pollinator network with  $n$  species in both communities, each pollinator species interacts preferentially with one plant species and with a lower probability with all other



**Figure 3:** Relationship between pollinator specialization and stability of plant-pollinator systems at four different levels of plant niche overlap. Community stability was defined as  $C = 1 - |\hat{\lambda}|$ , where  $\hat{\lambda}$  is the leading eigenvalue of the Jacobian matrix for the equilibrium at which all four species coexist. Results are shown for six different values of pollen carryover (parameter  $B$ ), the maximum number of flower visits between pollen removal and deposition, and for decreasing values of plant niche overlap with respect to abiotic resources ( $\gamma_{ik}$ ). The dashed horizontal line indicates the stability of a plant community without pollinators. Other parameter values used for this figure:  $\beta_p = 3.75 \times 10^{-6}$ ,  $\beta_A = 6.33 \times 10^{-7}$ ,  $d_p = 3 \times 10^{-8}$ ,  $d_A = 3 \times 10^{-7}$ ,  $b_{veg} = 3.5 \times 10^{-8}$ ,  $N = 1.1$ ,  $H_p = 10,000$ .

plant species, such that each plant is visited preferentially by one pollinator. Trait matching of a pollinator of species  $j$  with its preferred plant species  $i$  is calculated as  $\alpha_{ij} = (1/n) + [S(n-1)]/n$ , and trait matching with all other plant species  $k \neq i$  is calculated as  $\alpha_{kj} = (1/n) - (S/n)$ . Thus,  $\alpha_{ij} = \alpha_{kj}$  for a completely generalized network ( $S = 0$ ). In the most specialized network ( $S = 1$ ), each pollinator interacts exclusively with its preferred plant, hence,  $\alpha_{ij} = 1$  and  $\alpha_{kj} = 0$ . Note that this definition of specialization implies that a trade-off between specialist and generalist feeding behavior exists, that is, a generalist pollinator has a lower degree of trait matching  $\alpha_{ij}$  with each of the plant species it utilizes compared with the respective plant species' specialist pollinators. Although it is reasonable to assume such a trade-off (Egas et al. 2004; Sargent and Otto 2006), the general patterns presented below do

not qualitatively change without this assumption (see app. B).

## Results

Since all parameter values except trait matching were assumed to be equal for both species in a community, an equilibrium state with coexistence of all species was necessarily restricted to system states with exactly equal population sizes of both plant and both pollinator species. The effect of pollinator specialization  $S$  on the stability of this equilibrium varied with the degree of niche overlap of the two plant species with respect to abiotic resources (fig. 3): with a high degree of plant niche overlap (fig. 3A), coexistence in plant-pollinator systems was generally unstable. The rate of movement away from the coexistence equi-

librium after a small perturbation increased with increasing pollinator specialization. Whereas community stability of completely specialized systems ( $S = 1$ ) remained unaffected by pollen carryover, for systems with a lower degree of specialization ( $S < 1$ ), the speed of movement away from the equilibrium decreased with increasing pollen carryover. At an intermediate value of plant niche overlap (fig. 3B), coexistence remained unstable except for in highly specialized systems. Here the rate of movement away from the coexistence equilibrium was largest for intermediate degrees of pollinator specialization, but the difference between the stability of intermediate and more extreme values of pollinator specialization became less pronounced with increasing pollen carryover. With a further decrease in plant niche overlap, coexistence of the two plant and pollinator species became stable, at first only for specialized plant-pollinator interactions (fig. 3C) and then for all degrees of specialization (fig. 3D). At these low levels of plant niche overlap, a positive relationship was found between pollinator specialization and the return rate to the equilibrium after a perturbation. Higher degrees of pollen carryover resulted in increased community stability of systems with intermediate degrees of pollinator specialization.

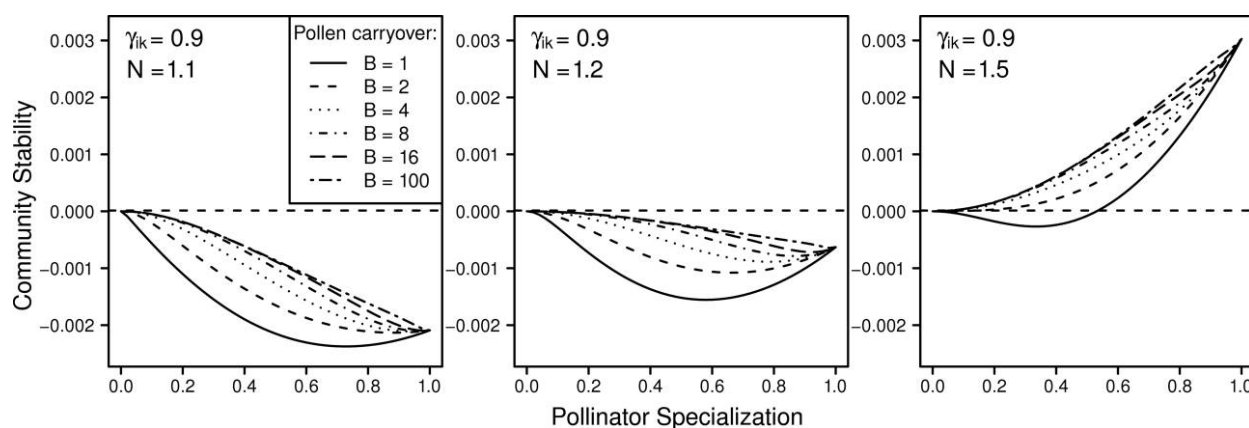
The absolute values of plant niche overlap ( $\gamma_{ik}$ ) that lead to a negative (fig. 3A), negative hump-shaped (fig. 3B), or positive (fig. 3C, 3D) relationship between pollinator specialization and community stability varied with the amount of nectar per plant ( $N$ ): with sufficiently high nectar amounts, stable coexistence and a positive relationship between specialization and stability existed even for values of plant niche overlap close to 1 (fig. 4). Increasing the rate of conversion of nectar to pollinator off-

spring ( $\beta_A$ ) or reducing the pollinator's mortality rate ( $d_A$ ) had the same effect as increasing the amount of nectar per plant (results not shown). These changes resulted in higher pollinator densities at equilibrium, while plant population densities remained unchanged. For example, with increasing nectar amount (fig. 4), the number of pollinator individuals per plant individual at the coexistence equilibrium changed from 0.61 (*left*) to 0.98 (*middle*) to 2.00 (*right*).

In comparison to the stability of a plant community without pollinators (dashed horizontal lines in figs. 3 and 4), plant-pollinator systems exhibited higher or lower community stability depending on the combined effects of all parameters mentioned above. Since completely generalized plant-pollinator systems ( $S = 0$ ) always had stability values of exactly 0 or lower, an increase in stability compared with that of a plant community with only vegetative reproduction required a certain degree of pollinator specialization. The same factors that resulted in increased community stability of plant-pollinator systems in general (see above) also facilitated greater stability of plant-pollinator systems in relation to a plant community without pollinators.

## Discussion

Whether certain types of interspecific interactions promote or impede species coexistence is a central question in ecological research. For mutualistic interactions between plants and pollinators, earlier studies predicted a reproductive disadvantage of less abundant plant species that would lead to the rapid exclusion of any initially rarer plant if no other factors halted its decline (Levin and An-



**Figure 4:** Effect of an increase in the amount of nectar per plant on stability of plant-pollinator systems. The relationship between pollinator specialization and community stability is shown for three different values of the amount of nectar per plant ( $N$ ), while plant niche overlap is kept constant at  $\gamma_{ik} = 0.9$ . All other parameter values are the same as in figure 3.

derson 1970; Waser 1978; Goulson 1994; Kunin and Iwasa 1996). Our quantitative analyses of community stability in plant-pollinator systems confirm this result. However, the destabilizing effect of pollination may be compensated by stabilizing mechanisms such as niche differentiation. Our results demonstrate that with sufficiently strong niche differentiation, interactions with pollinators may even increase the stability of plant species coexistence.

In our stability analyses, we analyzed system behavior in response to small perturbations from the equilibrium. For plant-pollinator systems with two species in each community, three different relationships between pollinator specialization and community stability were found: a negative relationship with high degrees of plant niche overlap, a unimodal relationship at an intermediate level of plant niche overlap, and a positive relationship when plant niches were largely separated. The situation at high levels of plant niche overlap corresponds to the case described by Levin and Anderson (1970) and others for generalized pollination. Here species coexistence is generally unstable, and a slight disturbance affecting a system at the coexistence equilibrium results in extinction of the initially rarer plant species. Interestingly, we found that species coexistence was unstable regardless of the degree of specialization of plant-pollinator interactions. The causes of this general instability become clear through a closer examination of the extremes of pollinator specialization.

In a system with two or more plant species sharing generalist pollinators, rare plant species receive as many visits on a per capita basis as more common species, but the probability of a visiting pollinator carrying conspecific pollen is lower for plant species with lower relative abundance. As a consequence, rare plant species produce a lower number of seeds per capita. If all plant species are almost equal in competition for space (i.e.,  $\gamma_{ik} \approx 1$  for  $i \neq k$ ), the probability that a plant of species  $i$  will establish at a given site is mainly determined by the proportion of all seeds produced by that species. Thus, plants of a less abundant species have fewer successfully established offspring per capita, and the species becomes successively more rare with each time step. The extent of pollen carryover determines the speed of extinction of a rare plant species. The higher the maximum number of flower visits between pollen removal and deposition (parameter  $B$ ), the smaller the reproductive disadvantage of a rare plant species.

When each pollinator species is completely specialized on a single plant species, the probability that a plant receives conspecific pollen is independent of its frequency in the community. However, a specialist pollinator of a rarer plant species must spend more time searching for its preferred plant; hence, its mean rate of nectar intake and its population growth rate are lower compared with

those of a pollinator specialized on a more abundant plant. As a consequence, the rare plant receives fewer pollinator visits on a per capita basis and produces fewer seeds than its more abundant competitor. This places the rare plant at a disadvantage in seedling competition for space. Thus, the situation creates a positive feedback that results in the rapid extinction of the plant-pollinator species pair. In plant-pollinator systems with an intermediate degree of specialization, rare plant species experience a mixture of the two different mechanisms that leads to reduced growth rates in completely generalized and specialized systems.

Whereas plant species without pollinators stably coexist as long as all  $\gamma_{ik} < 1$ , a higher degree of plant niche separation is necessary to overcome the minority disadvantage in plant-pollinator systems. As  $\gamma_{ik}$  decreases, the relationship between pollinator specialization and community stability changes from negative (highest rate of departure from the equilibrium at high degrees of pollinator specialization) to unimodal (highest departure rates at intermediate degrees of specialization). Here, the combined effects of both types of reproductive disadvantages experienced by rare species in specialized and generalized pollination systems lead to a faster decline of initially rarer species than either disadvantage alone. This strong effect in systems of intermediate degrees of specialization diminishes, however, with increasing pollen carryover.

At sufficiently low levels of plant niche overlap, species coexistence in plant-pollinator systems becomes stable for all degrees of specialization except completely generalized systems. In completely generalized plant-pollinator systems, community stability cannot rise above 0 because in this case, the two pollinator species are identical in all respects. Therefore, their coexistence is neutral. In a real ecosystem subject to environmental and demographic stochasticity, such a neutral community would slowly lose pollinator species through random ecological drift, until eventually only one species remains. Although the assumption of two or more pollinator species with exactly identical traits is somewhat hypothetical, our analyses show that stability of marginally specialized systems is also close to 0. With increasing pollinator specialization, the rate of return to the coexistence equilibrium after a small perturbation rises and becomes even larger than the return rate of a plant community without pollinators. Apparently, the increase in plant birth rates produced by interactions with pollinators leads to a faster recovery after a disturbance. Interestingly, whereas in a recent article Bastolla et al. (2009) found that generalized mutualistic networks allowed a maximum number of species to coexist, in our analyses community stability was maximized at high degrees of pollinator specialization. Whether this difference is due to the specific properties of pollination in comparison to other types of mutualism or a result of the



different measures of stability applied merits further investigation.

In our analyses, the degree of plant niche differentiation necessary to enable stable coexistence in plant-pollinator systems varied with the values of three parameters that influence pollinator growth rates: the amount of nectar per plant ( $N$ ), the rate of conversion of nectar to pollinator offspring ( $\beta_A$ ), and pollinator mortality ( $d_A$ ). The effects of these factors on community stability can be most easily understood by considering a system with two plant species  $P_i$  and  $P_k$  and perfectly specialized pollinators  $A_j$  (with  $\alpha_{ij} = 1$  and  $\alpha_{kj} = 0$ ) and  $A_l$  (with  $\alpha_{il} = 0$  and  $\alpha_{kl} = 1$ ). Here, even with niche differentiation of the two plant species and no interspecific competition between pollinators for food resources, the presence of  $P_i$  has an indirect effect on the pollinator of  $P_k$ : the higher the relative abundance of plant species  $i$ , the more time pollinators of species  $l$  need to spend searching for their preferred plant species  $k$ . Thus, if the relative abundance of plant  $i$  increases, the nectar intake rate of pollinator  $l$  may fall to a level where its birth rate cannot compensate for its mortality rate. In that case,  $A_l$  will decline and may become extinct if its birth rate at low density is still not high enough to balance its death rate. Increasing the amount of nectar per plant or the conversion rate of nectar to pollinator offspring or decreasing pollinator mortality allows a pollinator of a rarer plant species to survive under conditions that would otherwise result in its extinction. As long as the plant niches are sufficiently separated and  $b_{veg}$  is large enough to maintain a plant population in the absence of pollinators, plant species  $k$  will survive even if its pollinator dies out. On the other hand, if plant competition for space is strong, plant  $k$  may not be able to compete with plant  $i$  in the absence of its pollinator and may therefore also become extinct. However, our measure of local stability does not distinguish between these two cases.

Because we have now identified the degree of plant niche overlap and the three parameters affecting pollinator growth rates as the most important factors that determine the effect of plant-pollinator interactions on plant coexistence, it is clear that empirical estimates of these parameters are needed in order to draw conclusions about the stability of real plant-pollinator systems. As for plant niche overlap, very few studies provide experimentally derived estimates of Lotka-Volterra competition coefficients (Goldberg and Barton 1992; Silvertown 2004), a fact that may partly be due to the lack of a mechanistic basis of the Lotka-Volterra model (Chesson 2000; Dormann and Roxburgh 2005). However, since resource requirements and mode of resource use of different plant species within communities such as a meadow are often strikingly similar, it seems likely that levels of plant niche overlap close to 1 are the norm rather than the exception in natural plant

communities. Consequently, there is an ongoing debate about the question of whether differential resource use alone can explain coexistence of diverse plant communities even in the absence of a minority disadvantage mediated through pollination (e.g., Bell 2001; Silvertown 2004; Leibold and McPeck 2006; Levine and HilleRisLambers 2009). This raises the question of whether growth rate parameters of real pollinator populations are such that stable coexistence in plant-pollinator systems is possible even at high degrees of plant niche overlap. Rather than trying to find estimates for each parameter separately, it may be helpful to consider the fact that all three parameters affect the ratio of pollinators per plant at the coexistence equilibrium. To our knowledge, no estimates of this ratio have been published, but in a few cases the amount of flower resources required to rear a bee larva has been quantified (Müller et al. 2006 and references therein). These studies seem to indicate that the number of flowers needed to raise one bee varies widely, from less than one flower head of *Helianthus annuus* (Asteraceae) to several dozen flowers of *Campanula rapunculus* (Campanulaceae). Therefore, it may well be that the effect of interactions with pollinators on plant coexistence varies from one community to the other.

In conclusion, our analysis of population dynamics in plant-pollinator systems has shown that interactions with pollinators may impede or facilitate plant coexistence, and it identified a number of parameters that influence the stability of plant and pollinator communities. However, apart from the task of finding empirical estimates for these parameters, our approach has its limitations, and several open questions remain. For example, the measure of community stability applied here is just one of several possible choices (Grimm and Wissel 1997), and one that is based only on a system's behavior in the immediate vicinity of an equilibrium state. It would not be surprising if a measure that accounts for the effects of larger perturbations produced a different relationship between pollinator specialization and stability. Moreover, niche differentiation of plant species is by no means the only mechanism that may induce stable coexistence in plant-pollinator systems. From the literature, a number of other potentially stabilizing mechanisms are known that are not specific to plant-pollinator interactions but that can contribute to species coexistence in a variety of ecological contexts (Chesson 2000). Likewise, competition between pollinators could be modeled differently. In this model, pollinators do not compete for resources other than nectar. Thus, the strength of interspecific competition depends solely on the probability that two pollinators of different species visit the same flower. Inclusion of pollinator competition for other resources, for example, nesting sites for bees or larval host plants for butterflies, could affect the stability properties

of the system in several ways. Niche differentiation of pollinator species with respect to these other resources could have a stabilizing effect similar to that produced by plant niche differentiation. However, while populations of some pollinator species such as stem-nesting solitary bees may be strongly limited by the availability of nesting sites (Stefan-Dewenter and Schiele 2008), other important pollinator groups are unlikely to be limited by resources required for larval development. As a further group of mechanisms that contribute to species coexistence, other equalizing mechanisms besides pollen carryover could reduce the reproductive disadvantages of rare species in plant-pollinator systems. Some of these, such as flower constancy (Goulson 1994; Kunin and Iwasa 1996) or spatial aggregation of conspecific plants (Levin and Anderson 1970; Campbell 1986), were already mentioned by the authors of the articles that first pointed out the distinctive features of pollination and their consequences for species coexistence. While it is beyond the scope of this article to examine the differential effects of each of these factors, studying their relative importance for diversity maintenance may provide valuable insights to guide conservation efforts. Finally, the simple model systems with symmetric specialization examined in this study are of course an ideal.

In real pollinator communities, a mixture of different degrees of specialization is usually found. Our model provides the means to study the stability properties of real plant-pollinator networks in order to gain a deeper understanding about the relationship between interaction structure and robustness. This knowledge may help in making informed conservation decisions in order to preserve diverse plant-pollinator systems under rapidly changing conditions.

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## APPENDIX A

### Effect of a Holling Type II Functional Response on Community Stability

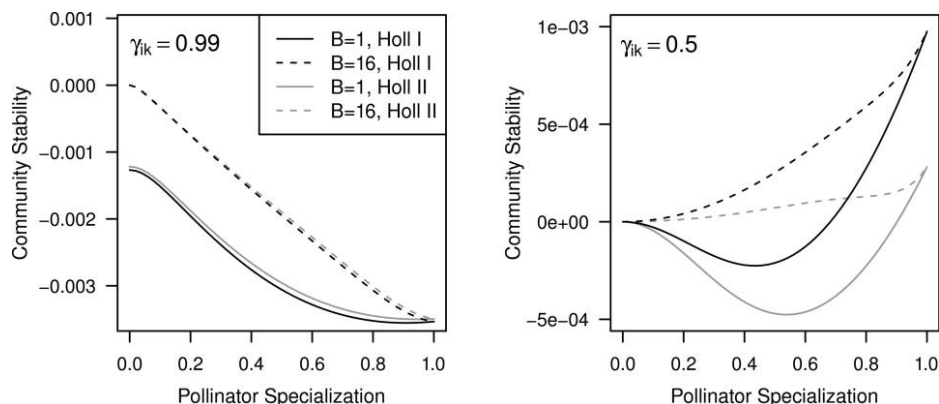
With saturating functional responses, the dynamics of plant ( $P_i$ ) and pollinator populations ( $A_j$ ) are described by the following equations:

$$\Delta P_i = \left( \frac{F_i S}{h_p + F_i} + b_{\text{veg}} \right) \left( 1 - \frac{\sum_{k=1}^m \gamma_{ik} P_k}{H_p} \right) P_i - d_p P_i,$$

$$\Delta A_j = \frac{R_j T}{h_A + R_j} A_j - d_A A_j.$$

Here,  $S$  and  $T$  denote the maximum number of seeds or pollinator offspring, respectively, that a single individual can produce within one time step;  $h_p$  and  $h_A$  are half-saturation constants. All other parameters are as defined in the main text.

The introduction of a saturating functional response for plant and pollinator reproduction did not induce a fundamental change in the relationship between pollinator specialization and community stability (fig. A1). However, a decrease in plant niche overlap from  $\gamma_{ik} = 0.99$  to  $\gamma_{ik} = 0.5$  had a stronger effect on a system with Holling type I functional responses. Otherwise, the effects of pollinator specialization and pollen carryover were identical.

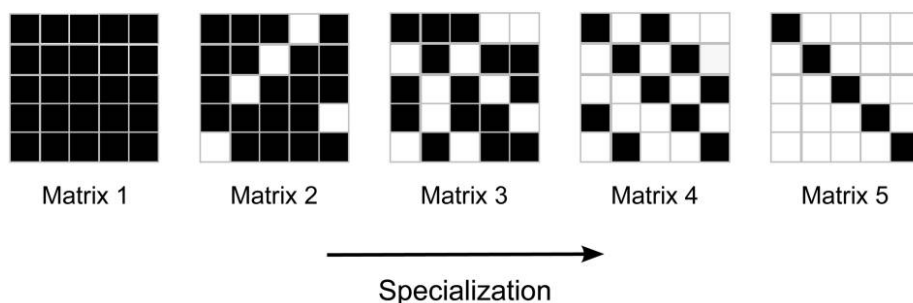


**Figure A1:** Effect of a Holling type II functional response on community stability. In both graphs, community stability of a system with two plant species and two pollinator species is plotted against the degree of specialization of plant-pollinator interactions for Holling type I (black lines) and Holling type II functional responses (gray lines) of both plant and animal birth rates. Results are shown for two degrees of plant niche overlap ( $\gamma_{ik}$ ) and two different values of pollen carryover (parameter  $B$ ). Community stability was measured as  $C = 1 - |\hat{\lambda}|$ , where  $\hat{\lambda}$  is the largest eigenvalue of the Jacobian matrix at the coexistence equilibrium. The following parameter values were used for this figure:  $S = 1 \times 10^{-5}$  and  $h_p = 2.6666$  or  $\beta_p = 3.75 \times 10^{-6}$ , respectively,  $T = 1 \times 10^{-5}$  and  $h_A = 15.5797$  or  $\beta_A = 6.33 \times 10^{-7}$ , respectively;  $d_p = 3 \times 10^{-8}$ ,  $d_A = 3 \times 10^{-7}$ ,  $b_{veg} = 3.5 \times 10^{-8}$ ,  $H_p = 10,000$ ,  $N = 1.1$ .

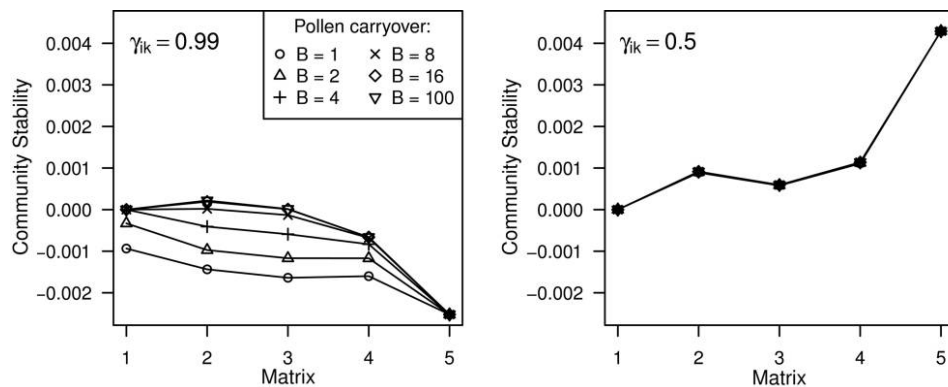
## APPENDIX B

### Relationship between Specialization and Community Stability without a Trade-Off between Generalist and Specialist Feeding Behavior

The measure of specialization of plant-pollinator networks,  $S$ , used in the main article implies that a trade-off between specialist and generalist interactions exists. In order to investigate whether the relationship between specialization and community stability would be altered without this assumption, we constructed matrices with  $\alpha_{ij} = 1$  for an existing interaction and  $\alpha_{ij} = 0$  for no interaction, and then we varied the number of interactions of each plant and pollinator species from a fully connected network to a network with exclusive one-to-one relationships (fig. B1). In accordance with the patterns found for networks with a specialist-generalist trade-off, at high levels of plant niche overlap the rate of departure from the equilibrium after a small disturbance increased with increasing network specialization (fig. B2,  $\gamma_{ik} = 0.99$ ). Likewise, community stability of generalized networks approached 0 for high degrees of pollen carryover, and a decrease in plant niche overlap resulted in a positive relationship between pollinator specialization and community stability (fig. B2;  $\gamma_{ik} = 0.5$ ). Thus, the qualitative results of the stability analyses presented in this article do not depend on the assumption of a trade-off between generalist and specialist feeding behavior.



**Figure B1:** Illustration of the method used to vary the degree of specialization of plant-pollinator networks without a trade-off. For the analyses presented in figure B2, matrices of trait-matching values ( $\alpha_{ij}$ ) for interactions between five plant and five pollinator species were constructed. The number of interaction partners per species was gradually reduced from five to one for successively more specialized networks. Trait-matching values were set to  $\alpha_{ij} = 1$  (black) for existing interactions and  $\alpha_{ij} = 0$  (white) for no interaction.



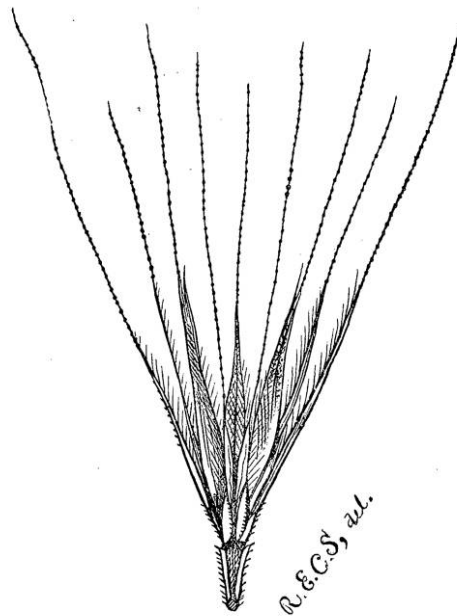
**Figure B2:** Community stability without a trade-off between generalist and specialist feeding behaviors. For the interaction matrices depicted in figure B1, community stability was calculated as  $C = 1 - |\lambda|$ , where  $\lambda$  is the leading eigenvalue of the Jacobian matrix for the equilibrium at which all species coexist. Results are shown for six different values of pollen carryover (parameter  $B$ ), the maximum possible number of flower visits between pollen removal and deposition, and two different degrees of plant niche overlap ( $\gamma_{ik}$ ). Other parameter values used for this figure are as follows:  $\beta_p = 3.75 \times 10^{-6}$ ,  $\beta_A = 2 \times 10^{-6}$ ,  $d_p = 3 \times 10^{-8}$ ,  $d_A = 3 \times 10^{-7}$ ,  $b_{veg} = 3.5 \times 10^{-8}$ ,  $N = 1$ ,  $H_p = 10,000$ .

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“Notwithstanding the browsing of cattle, the *Erodium* gained upon the previously conspicuous forms. Within the past two years, however, it has been losing ground, in some places more rapidly than in others, through the conquering advance of another plant, a form which, being not only worthless as food but repugnant to cattle, is not molested by them in its onward march for supremacy, which over large areas it has already achieved, to the nearly total exclusion of *Erodium*. This latter is what is known as barley-grass, or false barley, *Hordeum maritimum*, of which a spikelet is shown in the figure.” From “Form of Seeds as a Factor in Natural Selection in Plants” by Robert E. C. Stearns (*American Naturalist*, 1879, 13:411–420).