



The functional consequences of diversity in plant–pollinator interactions

Francisco Perfectti, José M. Gómez and Jordi Bosch

F. Perfectti (fperfect@ugr.es), Depto de Genética, Univ. de Granada, ES-18071 Granada, Spain. – J. M. Gómez, Depto de Ecología, Univ. de Granada, ES-18071 Granada, Spain. – J. Bosch, Unitat d'Ecologia, CREAM/Univ. Autònoma de Barcelona, ES-08193 Bellaterra, Barcelona, Spain.

The role of biological diversity in maintaining ecosystem functioning is a central issue in ecology. Most studies on diversity–functioning relationships have focused on ecosystem and community levels, leaving the extension of those relationships to other organization levels, such as populations, as a challenging and unsolved issue. Empirical studies have shown links between pollinator diversity and plant fecundity, suggesting that a diversity–functioning relationship at the population level may occur in pollination systems. We theoretically explored the effect of pollinator diversity on plant reproduction. We found that low pollinator diversity is beneficial when the most abundant pollinators are the most effective. In contrast, when the most effective pollinators are not the most abundant, we found an optimal value of pollinator diversity at which plant fecundity is maximized. When we parametrized our model with real data, we obtained that an increase in pollinator diversity was beneficial for the reproduction of some plants whereas it was harmful for other plants, the outcome depending exclusively on the differences in effectiveness among pollinators. Consequently, our theoretical approach suggests that in pollination systems the diversity–function relationship may be explained as the consequence of the interaction between among-pollinator differences in effectiveness and frequency of interaction, without the need to invoke additional ecological mechanisms.

The role of biological diversity in maintaining ecosystem functioning and services is a controversial but central issue in ecology and evolution (Kinzig et al. 2001, Loreau et al. 2002, Loreau 2008). Most experimental studies agree that species diversity has a positive, albeit saturating, effect on ecosystem functioning (Balvanera et al. 2006, Cardinale et al. 2006, Worm et al. 2006). Although most studies on diversity–functioning relationships have focused on the ecosystem and community levels, a challenging and still unsolved issue is determining whether the widely reported effect of diversity on system functioning can be generalized to other scales and organizational levels, such as population and individual levels (Bengtsson et al. 2002, Luck et al. 2003, Bascompte et al. 2006). The question then would be whether the functioning of these lower organization levels is affected by the diversity of the interactions they maintain. However, the analysis of the diversity–functioning relationship at the organismic level is hindered by demographic and genetic processes specific to this organization level. Under this perspective, the study of the diversity–functioning relationship becomes the study of the evolution of generalization–specialization in species interactions.

In plant–pollinator interactions, plants interact with animals that transport pollen and thereby can affect an important component of the plant's function, its reproduction. Pollinator diversity varies widely among plant species,

ranging from narrow specialization in plants relying on one or a few pollinator species to generalization in species pollinated by a wide array of animal species belonging to various taxonomic and/or functional groups (Proctor et al. 1996, Waser et al. 1996). In specialized systems, plants and pollinators are likely to develop tight co-evolutionary relationships. In contrast, the flowers of generalized plant species are visited by a variety of pollinators differing in both frequency of interaction and pollinating effectiveness (Proctor et al. 1996). However, there is no consensus so far on the benefit or detriment of being pollinated by a diverse versus a restricted array of pollinators (Waser et al. 1996, Gómez and Zamora 2006, Waser and Ollerton 2006).

Stebbins (1970) introduced the idea that specialization would be advantageous when pollinators differed in per-visit contribution to plant fitness (effectiveness). He assumed that, by modifying plant phenotype, natural selection would favor the attraction of high-effective pollinators and the deterrence of low-effective pollinators. Under these circumstances there would be a negative relationship between plant fitness and pollinator diversity and therefore, plant populations should evolve toward an increasing degree of specialization. This principle is commonly called the most effective pollinator principle (MEPP, Stebbins 1970, Proctor et al. 1996).

However, empirical data do not meet MEPP theoretical expectancies. In fact, many plant species have extremely diverse pollinator assemblages (Herrera 1988). In addition, a number of studies have reported ample variation in pollinator abundance and diversity (i.e. generalization) among plant populations (Ollerton and Cranmer 2002, Herrera 2005, Price et al. 2005, Gómez and Zamora 2006, Ollerton et al. 2006, Gómez et al. 2007, Petanidou et al. 2008), providing evidence that conspecific plant populations are subjected to broad variation in generalization, with different populations being pollinated by different numbers and identity of species. In addition, some studies have also shown temporal fluctuations in plant–pollinator interactions conducting to an underestimation of the generalization level (Petanidou et al. 2008). To overcome this contradiction between theory and data, some authors have suggested that generalization is possible when pollinators have equal effectiveness, being equivalent from a plant’s perspective, and when adaptations against ineffective pollinators do not produce a loss in the fitness contribution of effective pollinators (Aigner 2001, Gómez and Zamora 2006).

Furthermore, some empirical studies have found a positive relationship between plant functioning and pollinator diversity. For example, seed set of *Cucurbita moschata* and fruit set of *Coffea arabica* and *Coffea canephora* increases with pollinator diversity in Indonesia because of spatio-temporal niche complementarity (Klein et al. 2003a, 2003b, 2008, Hoehn et al. 2008). In California watermelon crops pollinator diversity was essential to conserve pollination services (Kremen et al. 2002), because of temporal changes in the bee species identity. Pollinator diversity increased seed production of *Raphanus sativus* and *Campanula glomerata* (Albrecht et al. 2007). In the wallflower *Erysimum mediohispanicum*, Gómez et al. (2007) found that populations produced more seeds at intermediate levels of pollinator diversity than at low or high levels.

In this study, we explore conditions producing the empirically observed relationships between pollinator diversity and plant fecundity. Previous studies have attempted to model the evolution of specialization/generalization in pollination systems (Waser et al. 1996, Aigner 2001) and to assess the importance of local species abundance in the evolution of pollinator attraction and plant specialization (Sargent and Otto 2006). However, these approaches have not specifically addressed the population outcomes of different generalization degrees. To advance in an integrated view of the consequences of generalization for plant populations, we have modeled the relationship between plant fecundity and pollinator diversity (a good estimator of generalization) at the population level. This approach allows us to simulate a diverse range of ecological situations, from plant populations being visited by very few species of pollinators to plant populations being visited by a high number of pollinators. Our computer simulations show that the effect of pollinator diversity on plant reproduction may vary from negative to positive depending on the differences among pollinators in effectiveness.

Material and methods

The model

Pollination may be considered a process with two components, one quantitative and one qualitative (Herrera 1987, 1989). The quantitative component refers to the frequency of interaction between a given pollinator and the plant, whereas the qualitative component refers to the fitness consequences for the plant when the interaction occurs (pollinator per-visit effectiveness). We have thus modeled the frequency and the effectiveness of pollinator assemblages differing in diversity, as well as the consequences to the plant in terms of female function. We have not considered changes in plant fitness via pollen transfer (male function).

Under this framework, the contribution of a given pollinator x to plant fitness is denominated its importance (Imp_x), and may be modeled as

$$Imp_x = FI(x) \times eff(x)$$

where $FI(x)$ is the frequency of interaction between the pollinator x and the plant and $eff(x)$ its pollinator per-visit effectiveness.

We have considered the frequency of interaction as the proportion of overall flowers visited by each pollinator species (or flower visitor in a broad sense) for a population of plants. The frequency of interaction for a given pollinator, in this sense, is an inclusive term summarizing pollinator abundance and visitation rate. We have modeled frequency of interaction as a gamma distribution. Multiple natural distributions have been found to fit gamma distributions (Azalee et al. 2006), which usually fit species abundance better than other distributions, such as the broadly used log-normal distribution (Schmidt and Garbutt 1985). The gamma distribution is described with two parameters: alpha, the shape parameter; and beta, the rate parameter. Maintaining alpha as a constant with value = 1, the gamma distribution is a continuous decreasing distribution, related to the negative exponential distribution, that ranking pollinator species from the highest ($x = 1$) to the lowest ($x = p$) frequency of interaction. By modifying beta, it is possible to modify the tail of the distribution and hence to change the pollinator’s frequency of interaction (Fig. 1).

Let

$$f(x; \alpha; \beta) = x^{(\alpha-1)} \frac{e^{-\beta x}}{\left(\frac{1}{\beta^\alpha}\right) \Gamma(\alpha)}$$

be the probability density function of the gamma distribution, where α is the shape parameter, β the rate parameter, Γ the gamma function, and x the rank order of a pollinator species, with pollinator species ranked from the highest to the lowest frequency of interaction. If α is assigned a value of 1, then this function could be written as:

$$f(x; \beta) = \beta e^{-\beta x}$$

This function is continuous but it can be discretized by solving this definite integral for x as a positive integer,

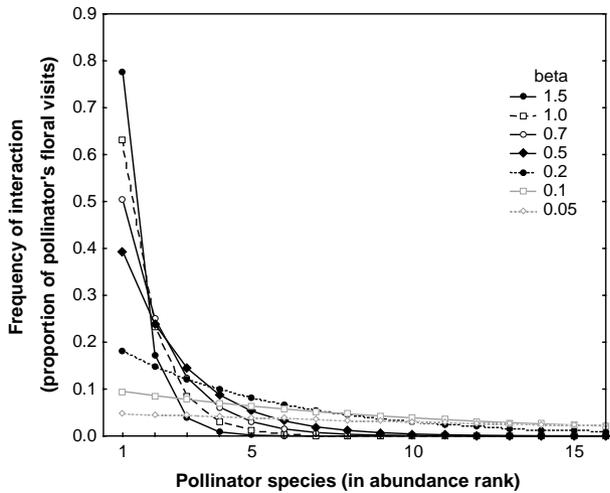


Figure 1. Different distributions of pollinator frequency of interaction (quantified as the proportion of flowers visited by each pollinator) modeled by changing the beta parameter of the gamma distribution. As the tail of these distributions could be shortened or elongated depending of the beta value, less or more pollinator species will be permitted to be in the distribution with non-zero values. From those distributions of pollinator frequency of interaction are possible to calculate pollinator diversity indexes. The actual values of those diversity indexes will depend on sample size. This approach assumes that the rank of each pollinator species does not change when beta is modified.

$$f(x; \beta) = \int_{x-1}^x \beta e^{-\beta x} dx$$

$$FI(x; \beta) = f(x; \beta) = e^{-\beta x}(e^{\beta} - 1)$$

producing an approximation to the frequency of interaction (FI) of a given pollinator species. It is also a gamma distribution for discrete values of $x \in [1, 2, 3 \dots p]$ where p is the pollinator with the lowest frequency of interaction. By modifying β , and sample size, this function allows to generate pollinator assemblages with different diversities.

Pollinator per-visit effectiveness depends on several factors, including the morphological fit between the flower's reproductive structures and the body of the pollinator, as well as a number of variables related to foraging behavior that ultimately influence the quantity and quality (allogamous, geitonogamous or xenogamous conditions) of the pollen deposited. Spears (1983) used an experimental approach to measure pollinator effectiveness, which he defined as the seed set by a plant population in response to pollinator visits. Spears calculated pollinator effectiveness $\frac{P_x - Z}{U - Z}$ where P_x is the mean number of seeds/flower by a plant population receiving a single visit from pollinator x , Z is the mean number of seeds per flower by a plant population without pollinators, and U is the mean number of seed/flower with unrestrained visitation (i.e. without pollen limitation). Here, for simplicity's sake, we will assume that $U=1$ and $Z=0$, and then pollinator effectiveness = P_x . We will use here a per-visit effectiveness with values between 0 and 1 representing no seed or full

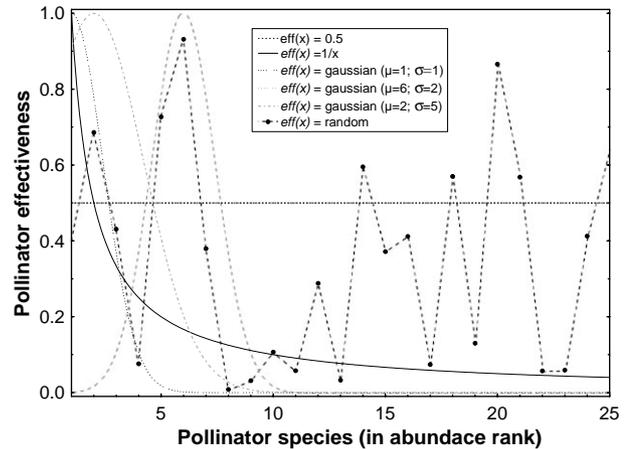


Figure 2. Several effectiveness functions (constant, decreasing, Gaussian, random) showing seed set production after single visits by each pollinator species ranked by frequency of interaction. One example of random effectiveness function is shown. The general term for these Gaussian functions is $eff(x) = e^{-\frac{(x-\mu)^2}{2\sigma^2}}$

seed set, respectively. We have not included plant phenotype variation in the model, allowing all plants to be pollinated with the same probability, i.e. our model is not evolutionary.

There are a number of effectiveness functions ($eff(x)$) potentially describing differences in effectiveness among the pollinator species visiting a plant species. These functions could be considered summarizing indexes of pollinator effectiveness (i.e. including all factors modifying pollinator effectiveness). We have considered four function types, according to the main scenarios proposed by experimental ecologists (Fig. 2).

- 1) A monotonically decreasing function, in which the most abundant pollinators are the most effective. For example, the following effectiveness function agrees with the MEPP (Stebbins 1970).

$$eff(x) = \frac{1}{x}$$

- 2) A continuous constant function, in which all pollinators have equal effectiveness.

$$eff(x) = \text{constant}$$

This effectiveness function assumes that all pollinators are functionally equivalent for the plant (Gómez and Zamora 2006).

- 3) A random function, with no relationship between pollinator abundance and effectiveness. This scenario agrees with some empirical reports (Fishbein and Venable 1996, Herrera 1996).
- 4) A family of unimodal functions in which the most effective pollinator is not necessarily the most abundant. For example, pollinator effectiveness could be described as

$$eff(x) = f(x; \mu; \sigma) = e^{-\frac{(x-\mu)^2}{2\sigma^2}}$$

This kind of effectiveness function follows a Gaussian distribution with mean μ and standard deviation σ , normalized with respect to the maximum value of $\text{eff}(\mu) = 1$. In addition, μ is the frequency of interaction rank of the most effective pollinator.

As mentioned, the importance of a given pollinator may be defined as the product of its frequency of interaction and its effectiveness. Under scenario 4, the importance of a pollinator x is defined as

$$\text{Imp}(x; \beta; \mu; \sigma) = e^{-\beta x} (e^\beta - 1) e^{-\frac{(x-\mu)^2}{2\sigma^2}}$$

or, simplifying, as

$$\text{Imp}(x; \beta; \mu; \sigma) = e^{-\frac{(x-\mu)^2}{2\sigma^2} - \beta x} (-1 + e^\beta)$$

We can differentiate this function to obtain

$$\text{Imp}'(x; \beta; \mu; \sigma) = e^{-\frac{(x-\mu)^2}{2\sigma^2} - \beta x} (-1 + e^\beta) \left(-\beta + \frac{\mu - x}{\sigma^2} \right)$$

and then solve $\text{Imp}'(x; \beta; \mu; \sigma) = 0$ to find the most important pollinator, i.e. the pollinator contributing the most to the fecundity of the plant population

$$X_{\text{MIP}} = \mu - \beta\sigma^2$$

Integrating Imp over the entire range of pollinators ($1 \dots p$), we obtain the theoretical mean population fecundity (\bar{F}_{pop}) of plants located in populations with pollinator richness $S_{\text{obs}} = p$, assuming no pollen limitation and no plant self-fertilization.

$$\bar{F}_{\text{pop}} = \int_1^p e^{-\frac{(x-\mu)^2}{2\sigma^2} - \beta x} (-1 + e^\beta) \left(-\beta + \frac{\mu - x}{\sigma^2} \right) dx$$

Following a similar procedure, the importance of the pollinators, their diversity, and the mean fecundity of the plant population may be calculated using other effectiveness functions. Some of these functions could not be algebraically solvable, but computer simulations allowed us to obtain insights to the process.

The computer simulations

To explore the consequences of pollinator diversity on plant population fecundity, we have simulated 1000 plant populations composed of $n = 500$ individuals, each with $f = 50$ flowers, and assuming no phenotype variation. Flowers were assumed not to self-pollinate. Each plant population was submitted to visitation by an assemblage of pollinators characterized by a given distribution of frequency of interaction and a given distribution of effectiveness. We have not introduced pollinator diversity indexes as parameters in the simulations, but calculated them after each flower was 'visited' (i.e. assigned) with one pollinator.

We modeled the frequency of interaction of each pollinator species using a gamma distribution as explained above. Pollinator species were assigned a numeric label following their frequency of interaction, e.g. the pollinator no. 2 is the second most interacting species. During the run of the simulations, each flower was assigned one visiting

pollinator, randomly drawn by sampling the gamma distribution ($\alpha = 1, \beta$). After the round of 'visits', we obtained for each plant population an $n \times f$ matrix containing the pollinator species visiting that population. From this matrix we can calculate several richness and diversity indexes for each population, such as S_{obs} , the observed pollinator richness, and PIE, the Hulbert's PIE diversity index (Hulbert 1971) measuring the probability that two randomly sampled pollinators pertain to two different species.

Each pollinator species was characterized by a per-visit effectiveness, which was modeled following the above-described four effectiveness functions (monotonic decreasing, constant, random and unimodal). Effectiveness values were allowed to vary between zero and one, with zero indicating no ovule fertilization, and one indicating full seed set per flower. For each set of simulations, we have maintained constant the effectiveness function and changed the frequency of interaction, which allow obtain different pollinator diversities in different populations.

To obtain plant fecundity, we assumed that each flower in a plant population produces seeds from 0 (no seed) to 1 (full seed set) depending on the effectiveness of the pollinator visiting that flower. Population fecundity (also varying between 0 and 1) is the average of the individual fecundities, and was obtained by substituting in the above-mentioned $n \times f$ matrix the identity of the pollinator visiting each flower by its per-visit effectiveness.

Simulations with data from real pollinator assemblages

In order to ascertain whether the relationship between pollinator diversity and plant fecundity produced by our theoretical approach appropriately describes plant-pollinator relationships in nature, we generated similar simulations but using empirical data. After searching the literature, we selected four studies in which per-visit effectiveness and frequency of interaction were measured for a moderate to high number of pollinator species. Herrera (1987, 1989) identified 58 species of pollinators visiting *Lavandula latifolia* (Labiatae) and, measuring stigma pollen loads after single visits, estimated the effectiveness of 26 of these species. In *Heterotheca subaxillaris* (Asteraceae), Olsen (1997) measured the frequency of interaction and effectiveness of 10 pollinator species as the percentage of receptive florets setting seed after single visits. Kandori (2002) characterized the abundance and effectiveness of 40 pollinator species of *Geranium thunbergii* (Geraniaceae) as seed set after single visits. Sahli and Conner (2007) estimated the effectiveness, as seed set after single visits, and relative abundance of 15 pollinators of *Raphanus raphanistrum* (Brassicaceae). For each of these studies, we ranked pollinator species based on their relative frequency of interaction and calculated relative effectiveness for each species. For each study, we simulated 1000 populations with different pollinator diversities, but without changing pollinator ranking. We assume zero effectiveness for those pollinators for which no effectiveness data were provided, either because it was not measured, or because no more pollinator species were observed. This assumption is conservative because it agrees with the MEPP predictions.

Results

Exploring the effect of the effectiveness functions

The relationship between pollinator diversity and plant fecundity varied widely depending on the pollinator effectiveness function used.

As expected, under the MEPP function, the simulations showed that the mean population fecundity decreased with pollinator diversity, irrespectively of the diversity index used (Fig. 3a). This occurs because increasing pollinator diversity encompasses an increment of inefficient pollinator visits. This outcome could be generalized to any decreasing effectiveness function (such as \sqrt{x} , $1/2x$, etc.) reflecting

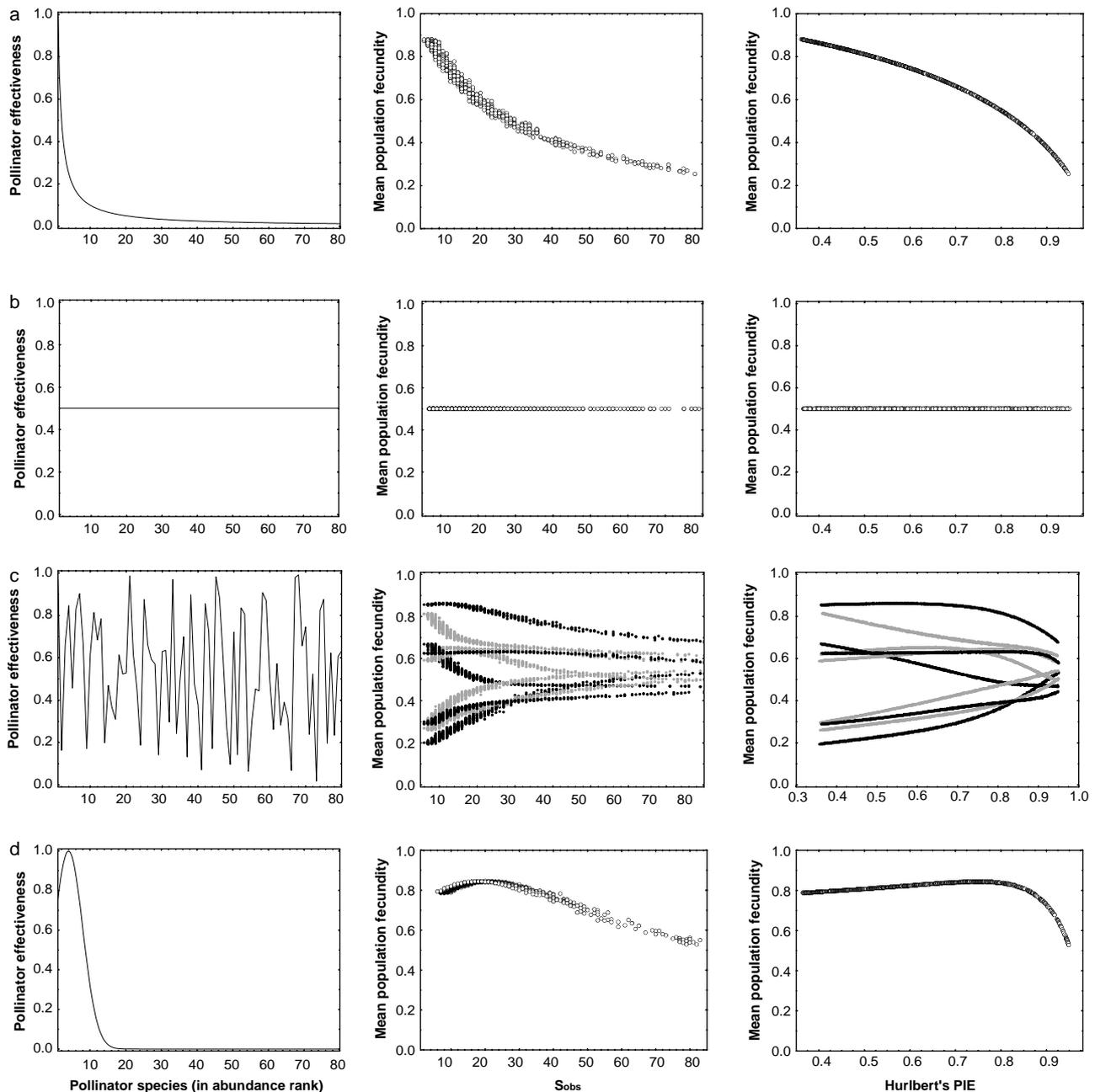


Figure 3. Relationships between mean population fecundity and pollinator species richness (S_{obs}) (second column) and Hulbert's PIE diversity index (third column), after the simulation of 1000 populations assuming a given effectiveness function (first column). In the first scenario (a), in which the effectiveness function follows a decreasing function (here represented as $1/\text{pollinator rank}$), mean population fecundity decreases with pollinator diversity. When effectiveness is identical for all pollinators species (b), mean population fecundity depends on the effectiveness value. When the effectiveness function is random (c) various outcomes are possible, some resulting in increases and others in decreases of mean population fecundity. Here we show the results of several possible random effectiveness functions (but only one random effectiveness function is depicted). At high diversities all curves converge to a mean population fecundity of 0.5. Finally, when pollinator effectiveness follows a Gaussian distribution with $\mu = 4$ and $\sigma = 4$ (d), mean population fecundity peaks at intermediate pollinator diversity.

situations where the most abundant pollinator is the most effective one (data not shown).

When pollinators are functionally equivalent (constant effectiveness function), plant fecundity did not vary with pollinator diversity (Fig. 3b). At population level, the expected outcome of this situation is the absence of a relationship between pollinator diversity and population mean fecundity.

The third explored scenario represents a random assignment of effectiveness to each pollinator species. In this case, a variety of outcomes are possible and plant fecundity may either increase or decrease with pollinator diversity (Fig. 3c). However, at high pollinator diversity, all functions tend to converge to a mean fecundity value of 0.5, coinciding with the mean value of a random distribution of pollinator effectiveness with range from zero to one.

In the fourth scenario, the effectiveness curve was modeled as a Gaussian function (defined by its mean and deviation). This allowed us to explore the effect of both the rank of the most effective pollinator (by changing the mean, which coincides with the rank of the most effective pollinator) and differences among pollinators in effectiveness (by changing the standard deviation term). The most simple situation, where $\mu = 1$ and $\sigma = 1$, is represented by a decreasing effectiveness function akin to the MEPP scenario (Fig. 4a). However, when the most effective pollinator is not the most abundant one, the relationship between pollinator diversity and mean population fecundity shows a maximum at an intermediate pollinator diversity level. The position of this maximum depends on the rank of the most effective pollinator (μ). When the most effective pollinator has an intermediate rank, maximum fecundity values are obtained at intermediate pollinator diversity ($\mu = 4$, Fig. 3d; $\mu = 5$, Fig. 4a). When the most effective pollinator has a high rank (low abundance), the relationship between pollinator diversity and plant fecundity first increases linearly and then plateaus at high values of diversity ($\mu = 10$; Fig. 4a). However, mean population fecundity is always lower when effective pollinators are scarce than when they are abundant (Fig. 4a).

We have also explored the effect of changing the variance in effectiveness while maintaining μ constant (as shown in Fig. 4b for $\mu = 4$). This amounts to modifying the number of pollinator species with effectiveness similar to that of the most effective species. A standard deviation (σ) = 1 indicates a huge difference between the first and the second most effective pollinator species. On the other hand, $\sigma = 10$ indicates that there are several pollinator species with effectiveness similar to the most effective one. Plant fecundity was lower at low σ values than at high σ values (Fig. 4b), indicating that it is beneficial to the plant to have equivalent high-effective pollinator species.

Simulations with data from real pollinator assemblages. Case studies

The simulations with the data from real plant species produce a variety of outcomes. The *Lavandula latifolia* study yielded a decreasing relationship between pollinator diversity and plant fecundity (Fig. 5a). In this species, the most abundant pollinator is highly effective and therefore

increases in diversity result in a strong decrease in plant fitness. The other three plant species yielded a unimodal relationship between pollinator diversity and plant fecundity (Fig. 5). In *H. subaxillaris*, we found an optimum of pollinator diversity at intermediate values of pollinator richness ($S_{\text{obs}} = 20$, $\text{PIE} = 0.767$) resulting in a maximum fecundity of 0.512 (Fig. 5b). This maximum represents a fecundity increase of close to 10% with respect to the situation with lowest pollinator diversity. This optimum was obtained despite the fact that pollinators over the 10th rank were assigned an effectiveness of zero. In *Geranium thunbergii*, we found an increase in population fecundity ($\sim 19\%$) with increased levels of pollinator diversity to unrealistic values of pollinator diversity ($S_{\text{obs}} = 81$) (Fig. 5c). In this species the most abundant pollinator was not very effective and the most effective pollinators were rare. Finally, in *Raphanus raphanistrum*, we found an optimum value of pollinator diversity when $S_{\text{obs}} = 46$ ($\text{PIE} = 0.903$), resulting in a 19% fecundity increase with respect to the minimal population fecundity ($F = 0.31$) at $S_{\text{obs}} = 12$ (Fig. 5d).

Discussion

Our study shows that the relationship between pollinator diversity and plant fecundity may vary from negative to neutral to positive, depending on the relationship between pollinator effectiveness and frequency of interaction. Although we have explored only a limited set of effectiveness functions, some general principles may be extracted. First, we found a negative effect of pollinator diversity on plant fecundity when the most abundant pollinators were those displaying highest per-visit effectiveness. When this occurs, it is beneficial to the plant to be visited only by the few most abundant pollinator species. This scenario fully agrees with the MEPP, which predicts the evolution of pollination specialization on the most effective pollinators (Stebbins 1970, Waser et al. 1996). Nevertheless, since our model is not evolutionary, we have not addressed the potential selection exerted by pollinators and the changes in the frequency of interaction associated with an increased attraction of the most effective pollinators. Theoretical models on the evolution of specialization and generalization have been addressed in other studies (Waser et al. 1996, Aigner 2001, 2006, Sargent and Otto 2006, Palaima 2007).

Our simulations also show that when pollinators have similar per-visit effectiveness, pollinator diversity does not affect plant fecundity. Under these circumstances, being visited by many pollinators is neither better nor worse than being visited by few pollinators. This situation of functional equivalence amongst pollinators may lead to non-adaptive generalization (Schemske and Horvitz 1984, Gómez and Zamora 2006). This scenario is unrealistic for highly generalized systems, because most studies have shown that pollinators widely vary in their effectiveness (Schemske and Horvitz 1984, Herrera 1987, Ashman and Stanton 1991, Olsen 1997, Gómez and Zamora 1999, Kandori 2002, Sahli and Conner 2007).

When effectiveness was assigned at random amongst pollinator species, and therefore no relationship between frequency of interaction and pollinator effectiveness existed,

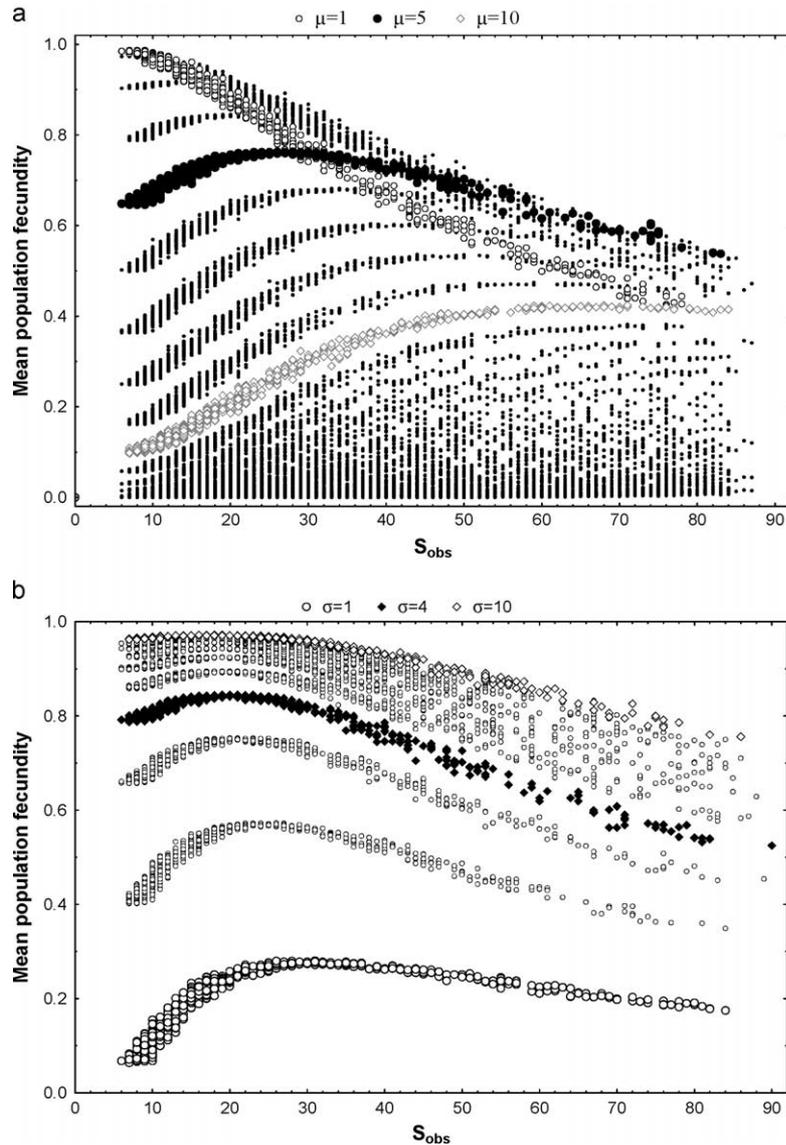


Figure 4. (a) relationship between mean plant population fecundity and pollinator species diversity assuming that the effectiveness function follows a Gaussian function (μ , $\sigma = 4$). Various outcomes are possible depending of the value of μ (rank of the pollinator species with the highest effectiveness). Curves for several μ values (1 to 15) are shown. (b) effect of variation in effectiveness among pollinator species on mean plant population fecundity. Curves represent results of simulations in which pollinator effectiveness was assumed to follow a Gaussian function with $\mu = 4$ and a range of standard deviation values ($\sigma = 1$ to 10).

the effect of pollinator diversity on plant fecundity ranged from positive, to neutral to negative. This occurs because in this scenario the effectiveness of the most frequent pollinators is not fixed but changes between simulations. Thus, if the most frequent pollinators are also very effective, it will be advantageous for the plant to be pollinated by a non-diverse pollinator assemblage. But if by chance the most frequent pollinators have low effectiveness, then being visited by few pollinator species will decrease seed production. Nevertheless, our models show that when pollinator diversity is very high, expected fecundity converges to 0.5 for all random functions. As a result, plants visited by an assemblage of pollinators showing no relationship between per-visit effectiveness and abundance may ensure an

intermediate level of seed production at high pollinator diversities. No relationship between frequency of interaction and per-visit effectiveness is expected in plant populations in which the identity and/or the abundance of the pollinators fluctuates unpredictably between years. This situation is equivalent to changing the rank of the pollinators without changing their effectiveness. According to our models, generalization would be a good strategy for a plant living in such a pollinator fluctuating environment, as it would consistently ensure an intermediate level of fecundity irrespective of pollinator fluctuation. High pollinator diversity would buffer against variations in the effectiveness of the most frequent pollinators. Temporal variation in pollinator fauna has been considered a main

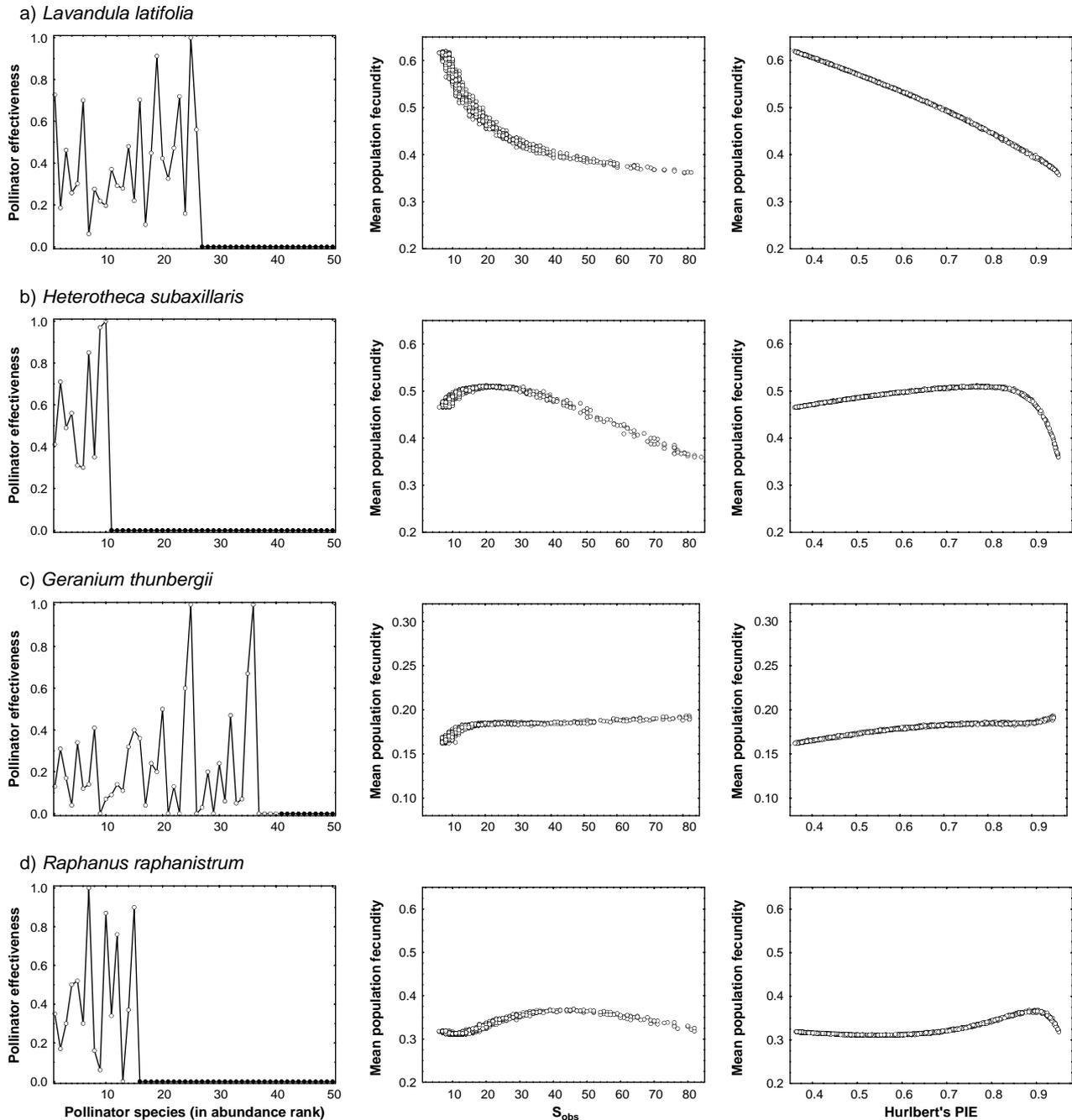


Figure 5. Relationships between mean plant population fecundity and pollinator species richness (second column) and pollinator diversity (third column) after the simulation of 1000 populations with effectiveness data of the pollinator assemblages of *Lavandula latifolia* (a) (Herrera 1987, 1989), *Heterotheca subaxillaris* (b) (Olsen 1997), *Geranium thunbergii* (c) (Kandori 2002), and *Raphanus raphanistrum* (d) (Sahli and Conner 2007). The relationship between pollinator effectiveness and frequency of interaction for each pollinator assemblage is also shown (first column). Effectiveness of pollinators not documented were assumed to be zero.

factor promoting generalization in flowering plants (Herrera 1988, Waser et al. 1996, Gómez and Zamora 2006).

We found that under certain specific conditions it is possible to find an optimal level of pollinator diversity maximizing plant fitness. According to our simulations with Gaussian effectiveness functions, when the most frequent pollinators have low effectiveness, an unimodal relationship between pollinator diversity and fitness is expected. This

theoretical outcomes agrees with some recent empirical results. For example, Kremen et al. (2002) found that the most effective pollinators of watermelon crops in California were those with intermediate abundance. Gómez et al. (2007) found an unimodal relationship between pollinator diversity and plant reproduction in the generalist crucifer *Erysimum mediobispanicum*. This results suggests that even for generalist plants there may be a cost of generalization if

the plant is visited by many low-effective pollinators. However, our simulations also suggest that this cost of generalization decreases as the most effective pollinators become less abundant. Under this scenario, it is beneficial to be pollinated by a diverse assemblage of pollinators. In fact, when the most effective pollinators are scarce, maximum plant fecundity occurs at so high diversity values that the relationship between pollinator diversity and plant fecundity becomes a linear positive function. Some recent studies have found a positive relationship between pollinator diversity and seed production or crop yield. For example, Hoehn et al. (2008) found correlative evidences linking pollinator diversity, but not abundance, to seed set in the pumpkin *Cucurbita moschata*. Greenleaf and Kremen (2006) have shown how changes in the foraging behavior of *Apis mellifera* mediated by the presence of wild bees (i.e. a higher pollinator diversity) improved seed set in hybrid sunflowers. In another study, Klein et al. (2003a) found a positive relationship between bee diversity and fruit set in coffee plants (*Coffea arabica*), illustrating the importance of conserving pollinator diversity to maintain adequate pollination services. This pattern is attributed to between-pollinator niche complementarity, both at temporal and spatial scales (Hoehn et al. 2008, Tylianakis et al. 2008). We propose that a similar functional pattern may arise as a consequence of the relationship between frequency of interaction and per-visit effectiveness of a pollinator assemblage. That is, a single mechanism can produce a relationship between pollinator diversity and seed production congruent with both the (evolutionary-oriented) MEPP and the functional equivalence scenarios, as well as the (ecosystem-oriented) positive scenario. It is important to note that when our theoretical approach was applied to data from real assemblages, we obtained very diverse pollinator diversity – plant fecundity relationships. This outcome suggests that it is possible to obtain a diversity–fecundity relationship even with the complex effectiveness functions found in the real world.

There are several mechanisms through which plant function (in terms of seed production) might be enhanced by pollinator diversity (Klein et al. 2008). One such mechanism is niche complementarity, which results in a more effective transfer of pollen in space and time. For example, some different pollinator species may preferentially visit flowers at different levels of the plant canopy (Johansen et al. 1982), and social bees are known to visit plants with high numbers of flowers compared to solitary bees (Willmer and Stone 1989, Klein et al. 2008). Different species may forage at different times of the day or the blooming period (Stone et al. 1998), or show different responses to weather factors resulting in climate-dependent complementarity (Vicens and Bosch 2000). Another mechanism explaining the relationship between pollinator diversity and seed production is functional facilitation. Interactions among species on flowers may force individuals to move from plant to plant more often, thus enhancing cross-pollination and resulting in higher seed production (Greenleaf and Kremen 2006). Interactions among pollinators need not be direct. Reductions in nectar levels caused by one species may cause other species to visit fewer flowers per individual again resulting in enhanced cross-pollination (Heinrich 1979). The amount of pollen remaining in the

anthers after the visit of a given species conditions the ability of another species to pick up pollen from that flower and therefore its pollinating effectiveness (Thompson and Thompson 1992). Finally, the increase in function with increasing diversity could be interpreted as a sampling effect, by which specious communities are more likely to include highly effective species (Ives et al. 2005). Our results show that this situation could also apply to some real pollinator assemblages, but other outcomes leading to different relationships can also occur.

Our simulations were conducted with a restrictive set of parameters and assumptions. First, our simulations considered a single pollinator visit per flower, a restriction that may be seen as non-realistic. Repeated visitation may result in processes such as stigma clogging or pollinator interference that could be important in natural populations. However, the effectiveness functions used in our simulations were inclusive in that they integrate most of processes shaping pollinator effectiveness. For this reason we do not think our conclusions would be significantly affected by repeated visitation. A second caveat of our theoretical approach is that it assigns pollinator visitation to all flowers. Nevertheless, in additional simulations (not shown), we varied the number of flower visited by pollinators. Decreasing the number of flowers visited only deemphasized the final differences among populations, but it did not change the general shape of the relationship between pollinator diversity and plant fecundity. A third caveat that limits the scope of our model is consider the plant as auto-incompatible. In the case of self-compatible plants, a high self-fertilization level, or if plants modulate autogamy in respond to low-effective pollinators, could produce that plants will compensate pollen limitation and, thereby, a flat relationship between pollinator diversity and seed production will be obtained. Finally, the model assumes constant and independent pollinator effectiveness and constant pollinator species rank order. Both assumption could be overstepped in nature. Pollinator interactions could, in some cases, improve seed set through changes in pollinator foraging behavior (Greenleaf and Kremen 2006) or can change pollinator frequency of interaction through pollinator competition (Fontaine et al. 2008). Temporal and spatial fluctuations in the pollinator community visiting a plant species have been widely reported (Ollerton and Cranmer 2002, Herrera 2005, Price et al. 2005, Gómez and Zamora 2006, Ollerton et al. 2006, Gómez et al. 2007, Petanidou et al. 2008). These fluctuations and interactions could change the relationship between pollinator diversity and seed set, implying that is possible to obtain similar diversity–fecundity relationships by different processes.

In conclusion, our study shows that when the most abundant pollinators are also the most effective, plants benefit from being visited by a low-diversity array of pollinators. However, when the most effective pollinators are not the most abundant, it is possible to find an optimal value of pollinator diversity maximizing plant fecundity. Several recent studies (Kremen et al. 2002, Ivey et al. 2003, Larsson 2005, Jauker and Wolters 2008, Madjidian et al. 2008) show that the most effective pollinators of many plant species are not necessarily the most abundant. According to our model, the occurrence of an unimodal relationship between pollinator diversity and plant repro-

duction may be more common than previously thought. In addition, our study suggests that in plant–pollinator systems, the shape of the diversity–function relationship may be explained as the consequence of the interaction between among-pollinator differences in effectiveness and frequency of interaction. However, other additional ecological mechanisms, such as niche partitioning, complementarity, or behavioral interaction among pollinators could also play an important role in explain those relationships.

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